Université Fédérale
Toulouse Midi-Pyrénées

THÈSE

En vue de l'obtention du

DOCTORAT DE L'UNIVERSITÉ DE TOULOUSE

Délivré par l'Université Toulouse 3 - Paul Sabatier

Présentée et soutenue par

Delphine DUCROS

Le 5 mars 2020

La dispersion dans un monde changeant: variations des coûts de la dispersion chez le chevreuil, et leurs effets sur l'évolution de la dispersion

---

Ecole doctorale : **SEVAB - Sciences Ecologiques, Vétérinaires, Agronomiques et Bioingenieries**

Spécialité : **Ecologie, biodiversité et évolution**

Unité de recherche :
CEFS - Laboratoire Comportement et Ecologie de la Faune Sauvage

Thèse dirigée par
Mark Hewison et Aurélie Coulon

Jury

M. Thierry Boulinier, Rapporteur
Mme Elise Huchard, Rapporteure
M. Jean-François Le Galliard, Examinateur
M. Stéphane Aulagnier, Examinateur
M. Mark Hewison, Directeur de thèse
Mme Aurélie Coulon, Co-directrice de thèse
M. Julien Cote, Invité

This PhD thesis is part of the project DISPCOST which has been funded by the Agence Nationale de la Recherche (ANR) (grant no. ANR-15-CE02-0008 obtained by A. Coulon). This PhD thesis has been realised at the Comportement et Ecologie de la Faune Sauvage (CEFS) lab, located within the INRA centre located in Castanet-Tolosan (Haute-Garonne), in partnership with the Centre d'Écologie et des Sciences de la Conservation (CESCO). It also includes a two-months exchange to the University of Aberdeen (Scotland).

This PhD thesis contains an introduction, a short material section focused on the study species and areas, four main chapters, including one published article in the journal Oikos, a general discussion and a references section. The entire manuscript is written in English, except for the Acknowledgement section.

“Courage doesn’t always roar. Sometimes courage is the quiet voice at the end of the day whispering, ‘I will try again tomorrow’” – Mary Anne Radmacher

Summary

Acknowledgements

Quelques jours avant le rendu de ce manuscrit, je me revois en deuxième année de Licence, assistant à la soutenance de thèse d'une doctorante au Muséum National d'Histoire Naturelle de Paris. Impressionnée par son travail, je ne me serais jamais imaginée être à sa place, préparant une thèse et la défendant, comme elle, devant un jury pendant trois bonnes heures dans l'Amphithéâtre de la Galerie de Paléontologie du MNHN. Cela me paraissait tellement haut niveau et loin… Et pourtant, sept ans plus tard, me voilà sur le point de terminer ma thèse sur la dispersion chez le chevreuil… Sept ans dont un peu plus de trois en particulier sur ce projet de doctorat. Et lorsque je repense à toutes les étapes parcourues, je ne peux m'empêcher d'être reconnaissante envers de nombreuses personnes qui ont accompagné ce chemin jusqu'à l'écriture de ce manuscrit. Je tiens à les remercier ici.

Tout d'abord, je tiens à remercier l'ensemble des membres de mon jury, Elise Huchard, Thierry Boulinier, Jean-François Le Galliard, et Stéphane Aulagnier qui ont accepté d'évaluer mon travail. Merci également à Julien Cote d'avoir accepté mon invitation pour assister à la présentation de mes travaux et pour nos échanges au début de ma thèse. J'ai hâte de pouvoir échanger avec vous sur la dispersion. Merci aussi à Stéphane pour les discussions toujours très enrichissantes au laboratoire et vos retours d'expérience.

Je souhaite ensuite remercier sincèrement mes trois encadrants de thèse, Aurélie Coulon, Mark Hewison et Nicolas Morellet. Déjà, merci infiniment à tous les trois pour m'avoir sélectionnée pour cette thèse. Ensuite, tout au long de ces trois ans, j'ai été très impressionnée par la rapidité de vos retours, votre efficacité, votre dynamisme, et je pense avoir beaucoup appris à vos côtés. Vous avez toujours répondu présents lorsque j'avais des questions et vous m'avez appris à pousser ma réflexion toujours plus loin. Un très grand merci à Aurélie, merci à toi pour ta disponibilité, et en particulier pour nos skypes toutes les semaines. Même si cela pouvait avoir un caractère intimidant en début de thèse, cela a été extrêmement bénéfique, et m'a fait progresser dans mon travail de façon efficace. Merci aussi pour tout ton soutien en fin de thèse, tu as été très présente et cela m'a aidée non seulement sur le plan professionnel mais aussi sur le plan personnel en fin de thèse. Tes encouragements ont toujours été vraiment très appréciés !! Merci Mark, pour tes conseils, les discussions au labo, sur le terrain, en déplacements, etc. et pour ta disponibilité quand je venais toquer à ta porte. Entre autres, tu m'as permis de mieux appréhender différents concepts d'écologie, et tu m'as appris à voir parfois les choses sous une autre perspective, alors merci à toi. Enfin, Nicolas, merci beaucoup pour tes conseils, sur les stats majoritairement, mais également pour tes relectures toujours très formatrices. Même si tu dis que parfois tu t'y connais moins dans un domaine, j'ai toujours trouvé tes remarques sur mon travail très pertinentes et enrichissantes, et encore une fois, tes retours m'ont aidée à pousser plus loin mes réflexions. Alors merci à tous les trois !

Merci également à tous les membres du laboratoire. En particulier, merci à Bruno L. pour toutes nos discussions sur le violon. Au final, discuter avec toi a fini par me faire accomplir l'un de mes rêves d'enfant, apprendre à jouer du violon ! Alors merci beaucoup à toi ! Je ne suis qu'à mes premiers pas de violon, mais quand je saurai un peu mieux jouer, on pourra jouer ensemble du Lindsey Stirling! ;)

Merci également à Cathy pour ta bonne humeur, nos discussions toujours passionnantes et tes multiples explications sur les ruches. Et merci beaucoup pour ton miel !! ☺ Discuter avec toi est toujours un très bon moment, enrichissant et vivant.

Un grand merci à Pascale, car le côté administratif, eh bien ce n'est pas toujours évident ! Merci pour ton efficacité, mais aussi un très grand merci à toi pour ton soutien après mon accident. En particulier, ton « Petit kit de survie en milieu hospitalier » m'a beaucoup touchée.

Merci à Lucie pour ta bonne humeur, ton ouverture, ton dynamisme et tous les moments sympas passés au labo. J'ai trouvé ça super chouette qu'une ancienne doctorante soit recrutée au lab*o,* car ça fait un peu comme une grande sœur de thèse, avec plein de conseils, alors merci à toi.

Merci à Georges pour nos discussions, notamment sur les grands prédateurs, et pour tous nos échanges lorsque l'on préparait nos activités de médiation scientifique à Toulouse et Paris. C'était chouette de faire ce projet de diffusion scientifique ensemble ! Merci également à Marianne et Bruno L. qui ont tout autant participé à ces évènements avec dynamisme. C'était un très bon moment !!

Merci à Yannick pour toutes les discussions à table ou en pause café. J'aime bien discuter avec toi, je trouve que tu as toujours un avis novateur et intéressant sur de nombreux sujets, alors merci pour ces discussions. Et merci bien sûr aussi pour ton aide sur le terrain personnalité ! Merci aussi à Bruno C., pour le terrain et tout ce que ça implique : suivre les chevreuils ensemble, t'écouter raconter tes anecdotes, croire tes blagues…. Ou que toi tu croies aux nôtres ! ;)

Merci aussi à Hélène, en particulier pour tous les moments terrain, notamment le traitement des échantillons après les captures ! Ca a toujours été des moments très sympas et conviviaux, notamment grâce à toi!

Merci à Denis pour ta bonne humeur au labo et sur le terrain, et tes blagues, j'ai beaucoup apprécié de faire du terrain en ta compagnie, et en particulier, merci de m'avoir initiée aux captures de chevreuils en première année !

Merci aussi à Erwan pour ta bonne humeur, ta curiosité et ton dynamisme ! Tout comme d'autres au labo, tu as contribué à faire des pauses repas des moments très sympas ! Merci à Joël pour les discussions à table, mais aussi pour m'avoir conseillée et aidée en première année avec mes problèmes de voiture (j'aurai appris l'utilité de changer une courroie de distribution !). Merci également à ceux que j'ai un peu moins côtoyés, mais qui néanmoins ont contribué à la vie du labo et à nos échanges scientifiques, Nicolas C., Jean, Marie-Line, Jeff, Jean-Luc, and Eric. En particulier, merci à Nicolas pour tes réponses aux petites questions que j'ai pu avoir sur toutes les opérations successives que tu fais sur la table de marquage, et merci à Jean pour ta gentillesse.

I also met great people outside the lab, in particular when I studied for two months in Aberdeen (Scotland). A special thank to Steve and Justin for welcoming me in your team, for our discussions, at the lab, at the restaurant or at the pub, and many thanks for your insightful advices throughout these three years. Thank you also to all the vibrant team, and in particular to Aurore, Rebekka, Beth, Vicinius and Greta. I had a very nice time with you all!!

Un très grand merci aussi à Jean-Michel Gaillard, à la fois pour votre présence dans mon comité de thèse, mais aussi pour vos conseils et votre très sympathique accueil à Lyon. J'ai beaucoup aimé échanger avec vous, et j'ai hâte de pouvoir poursuivre le travail avec vous sur le chapitre démographie de ma thèse !

Merci beaucoup à Rémi Choquet pour ses conseils sur les analyses démographie. Cela m'a beaucoup aidé !

Merci également à Patrick Mordelet et Eric Ceschia pour cette opportunité de donner des cours à l'Université avec vous ! C'était un réel plaisir de pouvoir participer à la diffusion de connaissances scientifiques aurpès des étudiants !

Merci aussi à l'équipe des doctorants, Ophélie, Laura G., Jeffrey, Alex, et Laura B. C'est toujours chouette de pouvoir avoir d'autres étudiants à proximité avec qui partager nos journées, discuter de nos analyses, faire des pauses sous le Soleil en été et prévoir des petites soirées pour décompresser. Merci Ophélie pour ton super accueil, pour toutes nos discussions, pour tes conseils quand je venais de découvrir l'écologie du mouvement, et ta bonne humeur ! ☺ Merci aussi à Laura B., mini Laura, pour ta présence finalement au labo quasiment depuis que j'ai commencé ma thèse ! C'était trop chouette que tu puisses faire ton M1, ton M2, puis démarrer ta thèse en même temps que nous poursuivions la nôtre avec Jeffrey et Laura G. Beaucoup de bons moments déjà passés avec toi et encore d'autres à venir ! ;) Merci aussi à tous les stagiaires qui sont passés par le labo, notamment Marie (On a tellement rigolé avec toi !!), Alexis, Marine, et Anaïs ! Merci aussi à Hugo, qui est arrivé dans la dernière année de thèse au labo. C'était super chouette de parler de voyages avec toi, de partager tes photos aux quatre coins du monde, profite bien du Sri Lanka ! Merci aussi à Alice, pour tous les moments sympas au labo, les discussions diverses et variées, mais aussi pour les restos en dehors ! ☺

Enfin, j'ai aussi eu beaucoup de chance lorsque j'ai commencé cette thèse, car le 1er octobre 2016, ce n'était pas seulement mon « premier jour », mais aussi celui de deux autres doctorants, Laura et Jeffrey. On a traversé ces trois années ensemble, et je voudrais ici tous les deux vous remercier. Laura, merci pour ton dynamisme, tes blagues, les petits airs que tu chantonnes, tes petites irruptions dans notre bureau. C'était super chouette que tu sois là pendant ces trois ans ! Au final, entre nos soucis de jambes respectifs on n'a pas trop réussi à aller danser ensemble, mais ce serait vraiment chouette qu'on s'y mette… un jour ! ;) Merci pour ton soutien, pour avoir été à l'écoute, et pour tes encouragements. Merci aussi pour ton aide et les discussions que l'on a pu avoir sur ma thèse. Plein de courage pour la fin !! Tu vas tout déchirer !

Jeffrey, merci pour … tout ! Hahaha ! En vrai, je crois qu'il n'y a pas meilleur colocataire de bureau ! ;) Merci pour ta présence, tes petits jeux de mots, pour avoir eu l'idée de mettre toutes ces plantes dans le bureau, pour nos petites pauses à regarder des caméras vidéos d'animaux à l'autre bout du monde ☺ Merci aussi pour ton soutien inébranlable, et pour tous tes conseils, en rédaction comme en stats. Merci aussi pour ton oreille attentive et ton soutien (toujours !) pour mes soucis d'accident et de rééducation. Je suis vraiment très reconnaissante de t'avoir retrouvé pour ces trois ans (et quelques^^) de thèse, et je te souhaite tout le meilleur pour le postdoc ! Mais avant, on va pouvoir se refaire plein de randos, de sorties, de repas… Et promis, on va enfin pouvoir regarder les Miyazaki !! ;)

I also want to thank all my supervisors from my previous internships or experiences, because it is undeniable that without your teachings, your advices and your shared experiences, I would not be writing this manuscript today. So, with a very thankful heart, I wish to thank Anne-Caroline Prévot, Colin Favret, Marco Musiani, Vivianne Lalanne-Bernard, Luigi Boitani et Paolo Ciucci, Alexandre Robert et Frédéric Jiguet. Many thanks too to Franck Courchamp, Corey Bradshaw and Céline Bellard for the great opportunity to work with you as a research assistant for a year, which truly was a very valuable experience for me. Many thanks also to all my « non-official supervisors » during fieldwork, and especially Joe Kermish-Wells, Christa Dubesky, Elisabetta Tosoni, Lorenzo Petrizzelli and Daniela Gentile. A special thank to Nicolas Loeuille, who was appointed to be my "referring teacher" when I just registered at the University. I have been so lucky that you were my referring teacher, first because you were an ecology researcher, and you gave me very valuable advices, but also because you were truly involved in your students future, and I was and still am very grateful for your listening ear and advices even though I was "just" a first-year student at the university among more than one thousand!

Passons ensuite à ma famille et mes amis. Tout d'abord, un très grand merci à mes parents, qui m'ont toujours soutenue dans mes études et qui ont passé un certain temps à me rassurer, depuis très jeune, lorsque je leur demandais « Tu crois que je vais y arriver… ? ». Merci Papa et Maman, car votre soutien a toujours énormément compté. Merci à Vincent et Clément, pour tous nos fous rires et nos délires. Merci pour vos petits messages, vos coups de fil et vos sourires, même à 2H du matin…! Merci à tous les quatre pour tous vos messages à la veille du rendu de ce manuscrit, cela donne de la force et fait chaud au coeur! Merci à toute ma famille au sens large, car tous m'ont soutenue et ont été compréhensifs lorsque je m'exilais pour travailler ;)

Merci également à toutes mes amies du lycée (ou d'encore avant ^^), et en particulier merci à Ju, Mélo, Titou, Léa et Laurine. Vous m'avez toujours encouragée, chacune à votre manière, on s'est organisé des défis pour toujours chercher à s'améliorer et progresser (plan BIB forever !!), et j'ai de la chance d'avoir des amies pareilles ! Merci Mélo et Ju en particulier pour vos petits textos quotidiens sur la fin de thèse, et Mélo pour tes poèmes !

Merci aussi à mes autres amis, ceux de Toulouse, qui m'ont vu leur parler de chevreuils avec les yeux pétillants d'énergie, ce qui les faisaient bien rire, puis qui m'ont un peu moins vue sur ces derniers mois... ^^ Merci Marine, Jean-Gab, Charlélie, Timothé, Maxime, Sarah pour votre présence, votre soutien, vos sourires et pour tous ces moments que l'on a passé ensemble !

Merci enfin à Bastien et ses parents, Gérard et Martine, pour leur soutien et leur présence ces trois années. Merci Gérard et Martine pour avoir été curieux de connaître le monde de la recherche et de la thèse, de chercher à comprendre les différentes étapes du doctorat, et merci pour votre soutien. Merci aussi de m'avoir accueillie tant de fois en weekend en Ariège. Ces weekends étaient des coupures inestimables pour moi, loin de l'agitation de Toulouse, et m'ont permis de travailler dans des conditions optimales, dans la nature, et chouchoutée avec de bons plats.

Enfin, merci à Bastien. Un immense merci à toi. Je pense que je ne pourrai jamais assez te remercier pour ta présence auprès de moi tout au long de ces trois ans. Tu as été d'un soutien indéfectible, tu m'as félicitée, encouragée, consolée, tu m'as appris à parfois, un peu, relativiser ^^ Merci pour nos ballades improvisées lorsque j'avais besoin de décompresser et merci pour avoir toujours discuté quand j'en avais besoin. Merci de t'être intéressé à ce que je faisais, à vouloir m'apprendre des

notions de SQL, ou à l'inverse, à t'intéresser à R. Merci pour m'avoir chouchoutée pour que je puisse me concentrer sur mon travail, tu as pris une sacrée avance en cuisine et ménage qu'il va falloir que je rattrape !! Enfin, merci d'avoir toujours cru en moi.

En arrivant à la fin de ces remerciements, je voudrais aussi remercier tous les petits chevreuils qui ont été suivis depuis des années, et qui m'ont permis de travailler sur de super données ! Ce ne doit pas être facile d'être capturés dans des filets, manipulés, échantillonnés, et ensuite suivis par d'étranges bonhommes verts à antennes… ! Merci donc pour votre participation, bien qu'involontaire à ma thèse et merci d'exister, car je vous trouve absolument trop mignons !! ☺

(En particulier 101 ;))


© adamfichna, Fotolia

Enfin, merci à mes trois petites boules de poils d'amour, Gribouille, Arwen et Ashitaka. A votre manière, vous m'avez toujours soutenue et donné du courage. Merci à tous les trois !

Introduction

Nowadays, our planet is facing major changes, which have already greatly modified the Earth. From mountains to rivers, from meadows to peat bogs and oceans, all ecosystems have been profoundly modified and damaged, mostly by human activities. Vitousek et al., in 1997, stated that approximately one third to one-half of the land surface had been transformed by human activities. Construction of cities, marine and terrestrial transportations, food and goods production have all led to deeply modified terrestrial and marine environments (Ramankutty and Foley 1998, Foley et al. 2005). Climate is also changing at a tremendous rate, linked with anthropogenic activities, and causing more frequent extreme climatic events, global warming, decrease in the amounts of ice and snow on the planet and sea level rise (IPCC 2014). These major changes are not without consequences for wildlife. Species extinctions are increasing with the current changes in landscape composition, human practices, species invasions, and ecosystems may become unstable because of anthropogenic modifications of landscapes (Pimm and Raven 2000, Reynolds and Peres 2006, Ceballos et al. 2015, Hautier et al. 2015). Moreover, the effects of global changes may be interactive, and together, accelerate the extinction process (Travis 2003, Brook et al. 2008).

In the face of these changes, only species which either demonstrate a sufficient level of plasticity to cope with novel environmental conditions, evolve in response to their new habitat characteristics or move away to find a suitable habitat will persist (Berg et al. 2010). Dispersal is one way to cope with these changes. However, large-scale anthropogenic changes are unprecedented in evolutionary history, leading to major modifications in resource distribution and abundance and landscape-associated risks (Harwood 2001, Backlund et al. 2008, Allen et al. 2010, IPCC 2014). Because current dispersal patterns did not evolve with these unprecedented environmental characteristics, dispersal patterns may not represent an adapted process anymore, or might evolve in an unknown way. Before covering how species might cope with global changes, including by dispersing, I first explain

which threats species are facing, to understand what role dispersal might play in mitigating these risks, and especially in the context of a changing world.

I- Era of global changes

1) Habitat destruction

Habitat destruction or degradation have been pointed out for a long time as having devastating effects on wildlife. They are defined as the extensive deterioration of a natural habitat from its original form and structure, with the consequence that this habitat is no longer able to sustain endemic species anymore (Fontúrbel et al. 2015). Habitat loss can go from partial fragmentation to the entire destruction of an ecosystem. Many factors can generate habitat loss, but most are linked to the growing human population.

a. Agriculture

Agriculture is considered to be the biggest cause of habitat destruction (Laurance 2010). In the face of the growing demand for more food, intensive agriculture developed strongly over the last three centuries, with a total global decrease of forested areas and woodlands of 1.2 billion ha, a decline by 560 million ha of grasslands and pastures, while croplands increased by 1.2 billion ha (Richards 1990). Foley (2005) estimated that crops and pastures now constitute one of the most represented biomes on the planet, with ~40% of the land surface occupied by these, to the detriment of forests and grasslands (Fig. 1). Tropical forests are particularly threatened by agricultural expansion (Gibbs et al. 2010). For example, palm oil production is held responsible for massive deforestation, especially in South East Asia, which strongly decreases species richness, especially in specialist species or in already endangered species (Fitzherbert et al. 2008). Increasing plantations not only destroy natural

landscapes for crops, but also lead to an extensive road network which gives access to previously

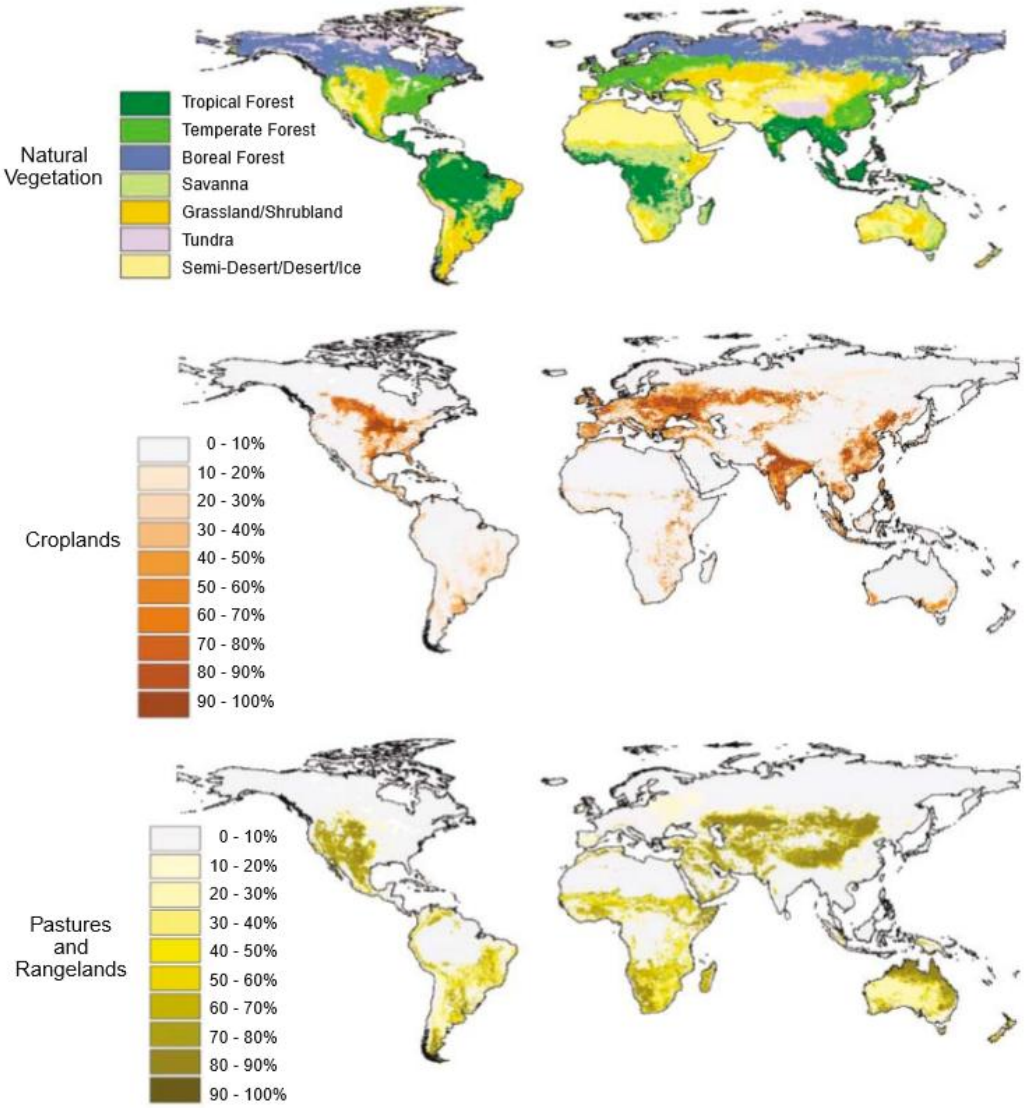


Fig. 1: Worldwide extent of human land-use and land-cover change. These maps illustrate the geographic distribution of ''potential vegetation'' (top), vegetation that would most likely exist in the absence of human land use, and the extent of agricultural land cover (including croplands and pastures) (middle and bottom) across the world during the 1990s. Figure from Foley et al. 2005.

wild areas for other types of activities (Laurance 2007, Taylor and Goldingay 2010). Tropical forests are not the only biomes which have suffered from habitat destruction (see Fig. 1 for an extensive list of major biomes impacted by human activities). Temperate and Mediterranean forests, for example, have also been strongly reduced in Europe, with 60 to 70% of these forests being lost prior to 1950

(Laurance 2010, Fig. 2). Intensive agriculture also encouraged the use of fertilizers and pesticides which have been proven to have devastating effects on biodiversity. Pollinators are particularly at risk. For instance, in Britain, the use of a fertilizer since the second half of the 19th century led to a decrease of wild flowers to the benefit of grass. Wild flowers are fundamental for many pollinating species, including bees and wasp, which use them for food and shelter, and thus, the use of this product led to strong pollinating population declines (Brown and Paxton 2009, Ollerton et al. 2014).

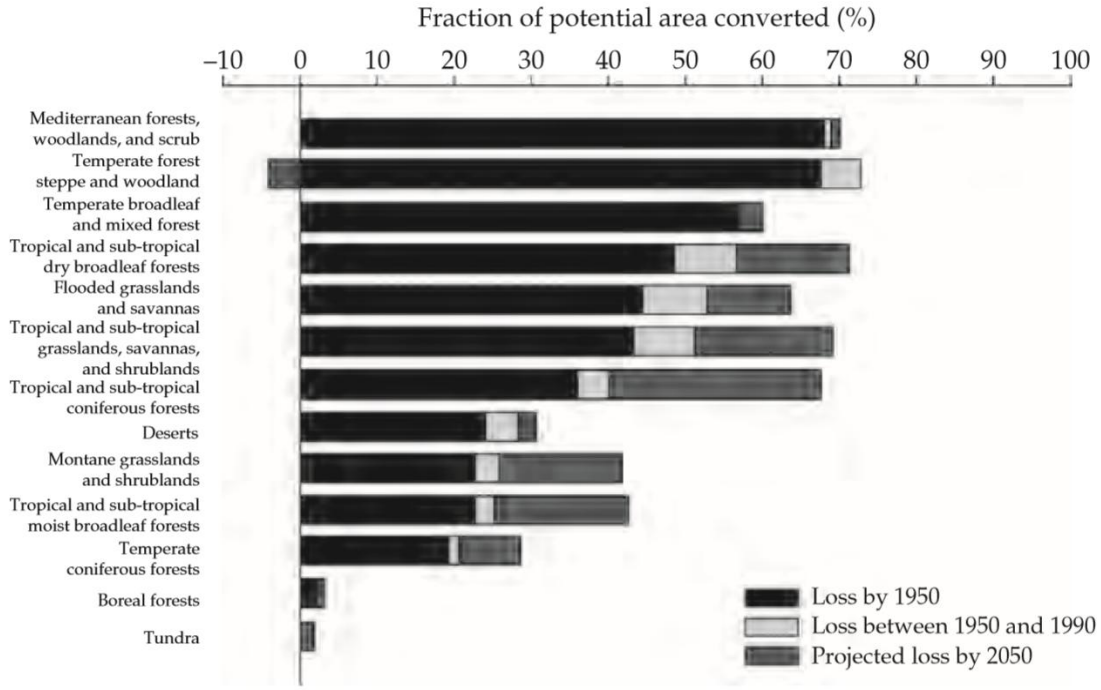


Fig. 2: Estimated losses of major terrestrial biomes prior to 1950 and from 1950 to 1990, with projected losses up to 2050. Figure from Laurance (2010) - Reprinted from MEA (2005).

b. Urbanization

Human population has grown extensively, especially in the last 200 years, and led to the need for more housing and infrastructures. The world's urban population is now estimated to 4 billion individuals, against 3.4 billion in rural areas (Ritchie and Roser 2019). Urbanization is the process by

which both human density and the intensity of their use of the habitat increase (Marzluff 2001). It constitutes a major modification of habitats by humans, and in most cases, is accompanied by a decrease in species richness in the area (McKinney 2008). Major urbanization examples are shown by the biggest cities, for example New York which was founded in the years 1800 and now constitutes a highly anthropogenized area. In big cities, natural habitats have been replaced by human infrastructures which do not necessarily provide the shelters and resources required for native species. For example, in Rome (Italy), the disappearance of green areas coincided with observed peak extinctions in insects, in particular coprophagous species because of changes in scat types in Rome (Fattorini 2011). Moreover, urbanisation leads to a homogenization of wildlife and the physical environment constituting the city, because cities are meant to fit the requirements of humans, but not necessarily those of the other species (McKinney 2006). The environment is not necessarily destroyed but can be highly modified. For example, public lighting was shown to impact courtship and reproductive success in two firefly species, with potential impacts on population dynamics and persistence (Firebaugh and Haynes 2016). Because humans often settle near aquatic ecosystems, the latter are also impacted by urbanization (Brown et al. 2005). For example, water pumping for human needs may cause or exacerbate local droughts and lead to fewer resources for aquatic species. Cities also release chemicals and heavy metals into the waters, and thus pollute the ecosystems more compared to smaller towns (Shinya et al. 2000). These releases may be detrimental for species which cannot survive with heavy loads of chemicals, or may modify community structures in coastal areas, sometimes leading to total anoxia and thus, death of local populations (Alves et al. 2011).

c. Mass energy production

Concomitantly with intensive urbanization and agriculture, mass energy and goods production have become prevalent in our society. For example, in China, rubber production has led to a reduction of tropical forests by about 67 % in 27 years (Li et al. 2007). Oil and gas production exploded in the last 150 years and are responsible for a massive degradation of the environment. Oil and gas

exploitations release particles which are toxic for organisms, can impact plant metabolism and may disrupt plant-water relationships (Ko and Day 2004). Because they remove habitat components on which species may depend, these exploitations are also considered responsible for the observed decline of species such as the woodland caribou (*Rangifer tarandus tarandus*) in Alberta. Indeed, these industries remove lichens and vegetation which are important for caribou habitat and create disturbances which caribou avoid (AWCRT 2005, Jones et al. 2015). Even if disturbed habitats may attract some individual species in some cases, for example wolverines, it can lead to subsequent mortality. For example, wolverines might incur more risks because they go near human activities to gain better foraging opportunities, and suffer from road-kills (Scrafford et al. 2017). Energy demand also impacts marine ecosystems, as they are used for energy as well, for example by the use of wind turbines which may cause a high mortality in seabirds. Moreover, sea is often used for goods transportation, and previous oil spills had major consequences on marine wildlife (Buskey et al. 2016).

d. Recreational activities

Lastly, habitats may also be modified for human's recreational activities in natural sites, which strongly increased recently, for example skiing, hiking, scuba-diving, or boating (Green and Higginbottom 2000, Balmford et al. 2009). Modifications of habitats to create the infrastructures necessary for these activities and accommodations (hotels, roads, transportations) can cause a lot of disturbance to species, including due to the presence of tourists themselves. For example, scuba-diving may cause disturbance to the species by touching them or simply by human presence, and may be responsible for an increase in coral death (Tratalos and Austin 2001, Milazzo et al. 2002). These habitat modifications have been proven to impact individual behaviours with potential fitness consequences. For example, grizzly bears avoid trails used by humans, especially those used for motorised recreational activities (Kasworm and Manley 1990, Ladle et al 2018, Fig. 3). This reduces

the possible areas where grizzly bears can forage, and leads to potentially lowered fitness, especially considering the energy allocated to avoidance behaviours.

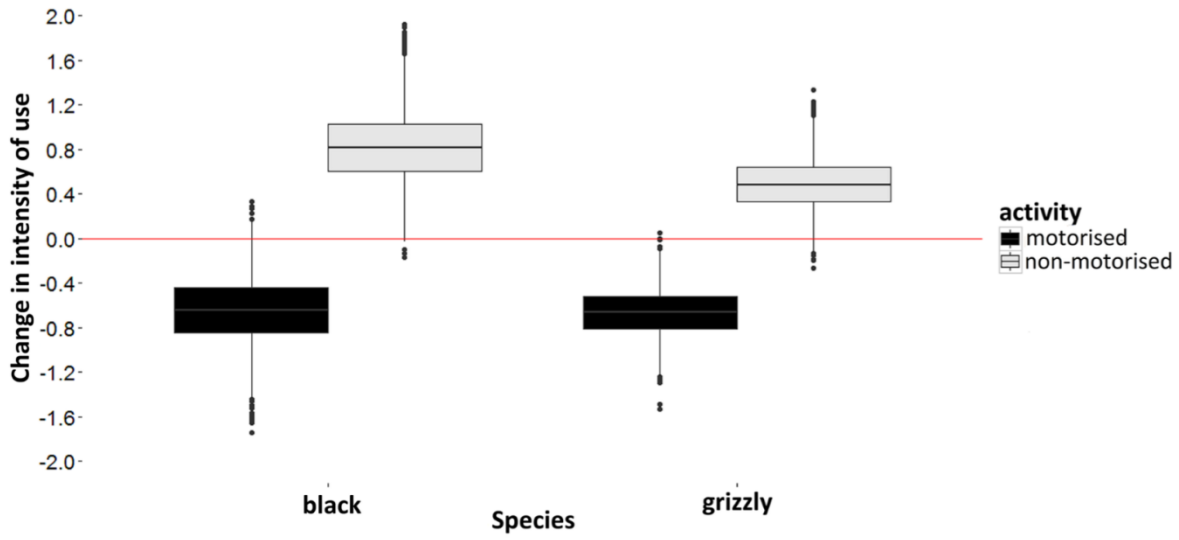


Fig. 3: Posterior distributions for change in intensity of use by grizzly bears and black bears due to the presence of motorised (black) and nonmotorised (grey) recreation (on the logit scale). The central mark represents the median, and the tails represent the 95% confidence intervals. Results were treated as non-significant if confidence intervals overlapped zero (red line). Figure from Ladle et al. 2018.

Yasué and Dearden (2006) directly showed a reduction in fitness in Malaysian plovers (*Charadrius peronii*), which suffered from a reduced reproductive success when tourism was high. In birds, an experiment showed that walking twice a day in the forest may have a negative impact on bird density and species richness (Bötsch et al. 2017). Lastly, species are part of a community, and thus, impacting one species may have cascading effects on other species. For example, wolf predation efficiency is increased when using anthropogenic linear features, which in turn is detrimental for caribou, which are already an endangered species (Dickie et al. 2017, Droghini and Boutin 2017). Lastly, disturbance may cause physiological alterations in several species. For example, drones flying over seabirds may provoke high levels of stress, especially in giant petrels and cormorants (Weimerskirch et al. 2018).

2) Climate change

a. What is climate change?

Climate change is now uncontested by most scientists: our climate is changing and this change will have detrimental effects on biodiversity (Dawson et al. 2011, Bellard et al. 2012). Climate change is characterised by major modifications in all climatic components, such as temperature, wind regimes, or precipitation (IPCC 2014, Fig. 4). It is mostly caused by an increase of greenhouse gases in the atmosphere, which is itself increasing because of the intensification of human activities (IPCC 2014). Greenhouse gases (for example, carbon dioxide, methane, nitrous oxide, fluorinated gases, ozone, water vapour, etc.) can also be called "heat-trapping gases", for they capture the radiation emitted by Earth, keep it as heat, and finally reflect it back towards the Earth surface (Karl et al. 2009). Because this phenomenon increased global temperature on Earth from ~ -18°C to the temperatures we currently register on Earth, it has allowed life to persist on Earth. However, the effects of human activities now unbalance the atmospheric composition in greenhouse effect gases, leading to a global warming of the Earth. Burning fossil fuels, deforestation, agriculture, livestock farming and transportation are all activities which lead to massive releases of greenhouse gases as well as aerosol particles which increase the warming effect on the atmosphere (Karl et al. 2009, IPCC 2014).

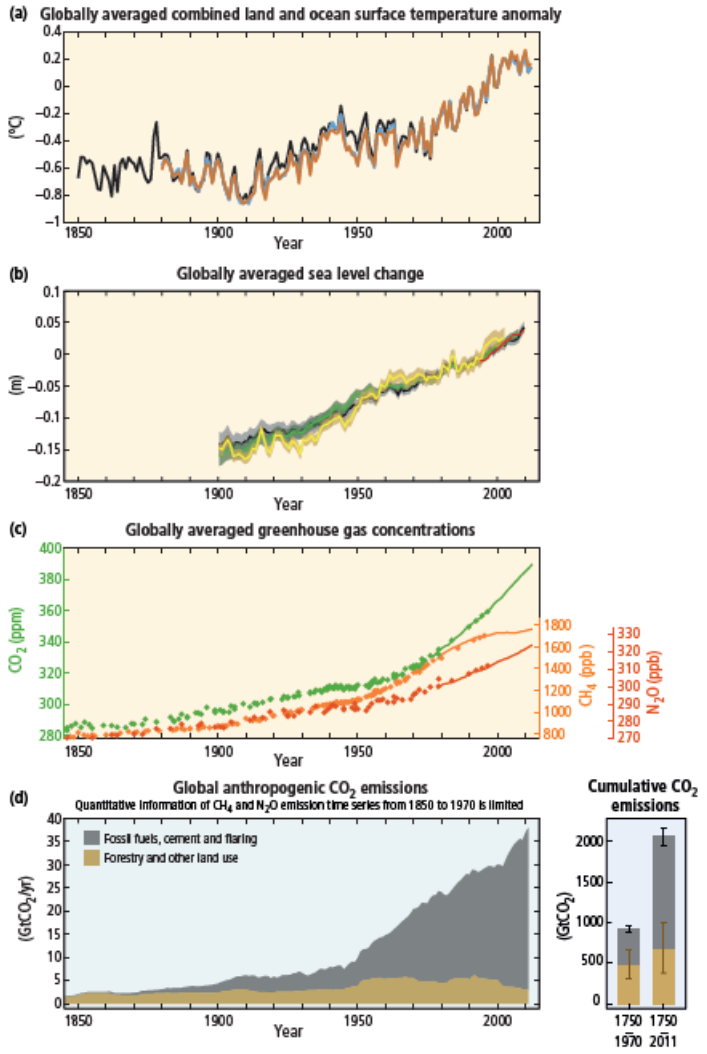


Fig. 4: Observations and other indicators of a changing global climate system. Observations: (a) Annually and globally averaged combined land and ocean surface temperature anomalies relative to the average over the period 1986 to 2005. Colours indicate different data sets. (b) Annually and globally averaged sea level change relative to the average over the period 1986 to 2005 in the longest-running dataset. Colours indicate different data sets. All datasets are aligned to have the same value in 1993, the first year of satellite altimetry data (red). Where assessed, uncertainties are indicated by coloured shading. (c) Atmospheric concentrations of the greenhouse gases carbon dioxide (CO2, green), methane (CH4, orange) and nitrous oxide (N2O, red) determined from ice core data (dots) and from direct atmospheric measurements (lines). Indicators: (d) Global anthropogenic CO2 emissions from forestry and other land use as well as from burning of fossil fuel, cement production and flaring. Cumulative emissions of CO2 from these sources and their uncertainties are shown as bars and whiskers, respectively, on the right hand side. The global effects of the accumulation of CH4 and N2O emissions are shown in panel c. Figure from IPCC 2014.

b. Consequences of climate change

Global warming has consequences on both terrestrial and marine ecosystems. On land, increasing temperatures can lead to local droughts and hotter environments, but also changes in atmospheric circulation patterns and humidity. This may in turn affect precipitation regimes: in consequence, drought episodes may be even more intense, or on the contrary, recurrent flooding may occur depending on the region on Earth (Milly et al. 2002, Karl et al. 2009, Allen et al. 2010, Dai 2013). Higher temperatures can lead to a decrease in reproduction, survival and dispersal, as well as changes in physiology. For example, in California, drought has led to a lowered primary production, leading to fewer insects, and thus, less nutritive resources for four passerines birds which have incurred lower reproduction success (Bolger et al. 2005). Increasing temperature is also suspected to increase mortality rates, for example in moose, because of increased spread of diseases and parasites when temperature regimes change and a global body deterioration in moose with heat stress (Murray et al. 2006, Lenarz et al. 2009). Occupancy and population range may also decrease because of higher frequencies of droughts, as has been the case for a population of koala in Queensland, Australia (Seabrook et al. 2011). Climate change may also lead to changes in phenology in many species, but some may not succeed in shifting their phenology simultaneously with climate change and also with the community they live with, and thus individuals may incur reduced fitness (Visser and Holleman 2001, Edwards and Richardson 2004, Visser and Both 2005, Berg et al. 2010). Warming also increases ice melting and leads to more 'rain-on-snow' events, during which snow is covered by ice, limiting access to nutritive resources for herbivores (Stroeve et al. 2014, Descamps et al. 2017). In oceans, climate change has a strong effect on sea level rise and ocean acidification (Doney et al 2012). Indeed, an increase in water temperature increases water density, which thus expands (Mitchum et al. 2017). Moreover, glacier ice on land is also melting and adds to the amount of water already present in oceans. As a consequence, the sea level has increased by 0.19 from 1900 to the end of the 20th century, and might still be growing (Church et al. 2013, Rhein et al. 2013). Sea level rise may have detrimental effects on habitats such as coral reefs and decrease connectivity, for

example between islands (Karl et al. 2009). Rising temperatures in the ocean may also be responsible for stronger and more frequent hurricanes in some regions of the world, including the eastern Pacific and the Atlantic oceans (Karl et al. 2009). Atmospheric concentrations in CO_2 also led to a reduced pH in waters, and estimates from the Intergovernmental Panel on Climate Change (IPCC) predict that ocean's acidity may increase by about 150% by the end of the century relative to the beginning of the industrial era (Feely et al. 2009). This increased acidity is also characterised by a decrease in calcium carbonate, which will have detrimental effects on calcium-secreting organisms, such as echinoderms, bivalves, coral and crustacean species, including on fertilization, larval development, skeletal-growth rate, mortality rates and reproduction (Kurihara 2008). Warming waters are also having direct effects on organism physiology, for example increasing metabolic rates (Hoegh-Gulberg and Bruno 2010), and can modify species interactions, including predation (Hoegh-Gulberg et al. 2007, Harley 2011). These alterations may in turn have important consequences for community structure and ecosystem functioning (Walther 2010). Because of all the above-cited effects it may generate, climate change is predicted to lead to massive extinctions both in terrestrial and marine ecosystems (Thomas et al. 2004a, Cheung et al. 2009, Bellard et al. 2012). Moreover, interactions between species within communities may trigger cascading extinctions (Koh et al. 2004).

3) Overexploitation of species, pollution and species invasions

Apart from habitat modifications and climate change, three other threats are implicated in species declines. Because these three components will not be studied in this PhD thesis, they will only be briefly presented here.

a. Overexploitation

Today, species are largely overexploited across the planet for food, fiber, medicine or because of conflicts with humans (Reynolds and Peres 2006). Overexploitation is defined as the intense use of an animal or plant species for humans' needs which is not sustainable for species maintenance. Many

species have been threatened or are currently threatened by man because they constitute a food resource. For example, industrial fishing occurs in more than 55% of the oceans (Kroodsma et al. 2018), and overexploitation of fish resources is a strong threat not only for targeted fish (for example tuna), but also non-target species, such as dolphins, sea turtles, seabirds and sharks (Rosenberg 2003, Reynolds and Peres 2006, Gilman 2011). Other types of overexploitation include hunting. For example, in Ghana, 41 mammal species are threatened by bushmeat hunting (Brashares et al. 2004), especially when human's primary protein source, fish, is poor. Moreover, wildlife also suffers from illegal killing, for traditional medicine or gourmet dishes (Challender 2011 for pangolins, Liu et al. 2011 for Asiatic bears, Biggs et al. 2013 for rhinos, Kamp et al. 2015 for Yellow-breasted buntings). Terrestrial species are also impacted by by-catch mortality (i.e. non-intentional mortality on untargeted species while hunting or catching other targeted species) including elephants, lions and African wild dogs (Becker et al. 2013). Large-scale hunting of particular species has also participated to extinctions or massive declines, such as for Passenger pigeons, or predators whose biological requirements overlap with those of men, for example brown bears or wolves (Woodroffe 2000, Hung et al. 2014).

b. Pollution

Linked to increased urbanisation and intensification of agriculture and energy production, ecosystems have been increasingly polluted by anthropogenic activities in the last centuries. Pollution is defined as the introduction of materials or particles, directly or indirectly through human activity, and susceptible to alter ecosystem quality and the health of organisms living in these ecosystems (Newman 1979, Newman and Schreiber 1988). Many studies have now shown pollution and its impact on wildlife. On land, massive use of fertilizers, pesticides, and other chemical products to increase crop yield has highly polluted soils, streams and biodiversity (Foley et al. 2005). For example, the use of neonicotinoids, an insecticide widely used in crop fields, has been accelerating bird decline, presumably because of its negative impact on insect populations (including non-target

species) and modifications of soil and water properties (Goulson 2014). Light pollution coming from cities, roads, and other human infrastructures can also have drastic impacts on species accustomed to navigate in a dark environment (for example, bats or sea turtles), which may not be able to attain the habitat or resources they need (Longcore and Rich 2004). Light pollution at night was also found to impact both reproductive success and survival in *Drosophila melanogaster* (experimental study, McLay et al. 2017), and the selectiveness of female frogs for a male partner (Rand et al. 1997), reducing fitness in both cases. At sea, plastic pollution is devastating marine wildlife, with individuals entangled in nets, suffering from corrosion by plastic elements, eating pieces of plastic taking them for food, and accumulating plastic particles which will impact their health over time. Over 170 marine species may be ingesting plastic bits, with serious consequences such as digestive track perforation or starvation (Vegter et al. 2014, Wilcox et al. 2015). Moreover, additional water pollution comes from particles and waste rejected by urban areas into streams. Even if this type of pollution has been reduced out of concern for human health, it is still particularly threatening for aquatic wildlife (Wang and Peng 2001, Cadenasso et al. 2008, Paetzold et al. 2011).

c. Invasive species

Lastly, invasive species are causing major declines all across the globe (Bellard et al. 2016). Because of large-scale human movements across the planet, many species have been transferred deliberately or inadvertently from their original habitat to a new location (Mooney and Hobbs 2000, Simberloff 2010). Some of them have become invasive, as they adapted to their new range and exploited its resources to the detriment of local species. Island species are of particular concern because they have evolved independently from continental environments, and thus, may not be able to adapt to habitat modifications. For example, the introduction of feral cats (*Felis catus*) on islands has contributed to at least 14% of bird, mammal and reptile extinctions (Medina et al. 2011). Some ground-nesting species are especially vulnerable to cat predation because their nests are accessible to any terrestrial predator. In Europe, the introduction of American grey squirrels (*Sciurus*

carolinensis) is threatening the native red squirrel (*Sciurus vulgaris*) because it is more competitive and forages for nuts more efficiently (Bertolino and Genovesi 2003, Gurnell et al. 2014), although grey squirrel may be currently decreasing in some parts of their European range (Flaherty and Lawton 2019). As for the previous threats cited above, invasive species (especially plant species) can also alter ecosystem processes (Vitousek et al. 2017).

II- How species may cope with global changes

1) Species adapt…

In the context of current global change and its many threats, species need to adjust to their environment to persist or move away from it (Berg et al. 2010). Their adjustment can either come from phenotypic plasticity or genetic adaptation, also called microevolution (Pulido and Berthold 2004). Phenotypic plasticity consists in the ability to express different individual phenotypes (behaviour, morphology or physiology) in response to alternative environmental conditions. These modifications thus result from the direct influence of the environment, may be reversible or not, and allow an organism to adapt to a set of environmental conditions for which the different phenotypic responses may be adaptive (Pulido and Berthold 2004). However, with the ever changing environment, phenotypic modifications an individual may adopt might become insufficient or maladaptive because plasticity is restricted to a delimited range of variation, and the expected fitness for that individual may decrease (Coppack and Pulido 2004, Chevin et al. 2010). Moreover, phenotypic plasticity also incurs some costs and limits, which may prevent organisms to respond to environmental changes (DeWitt et al. 1998, Murren et al 2015). On the other side, genetic adaptation may allow species to adapt to all sorts of environmental modifications, but it is a slow process and it needs additive genetic variance for the trait under selection to produce phenotypes adapted to the environment. Thus, genetic adaptation may only have a role in species response to

environmental change if the pressure incurred in the presence of global changes is sufficiently low to allow for populations to persist in the meantime. In both cases, adaptation relies on the available traits acquired through evolutionary history (Sih et al. 2011). Because our planet is changing at an unprecedented rate, which is too fast for genetic adaptation to occur in numerous cases, it seems that phenotypic plasticity prevails over microevolution, even if both are not mutually exclusive and few studies actually studied genetic adaptation using genetic data (Gienapp et al. 2007, Hendry et al. 2008, Berg et al. 2010, Charmantier and Gienapp 2013). Indeed, both types of adaptation are contributing to observed changes in animal phenotype and may be hard to disentangle (Bradshaw and Holzapfel 2006; Parmesan 2006, Gienapp et al. 2007).

a. Phenotypic plasticity

Individuals may modify their phenotype by acting on three main components: behaviour, phenology and physiology, depending on the expression of global change they are incurring. As previously explained, habitat modifications and destruction may cause species disturbance, to which the latter may respond by modifying their habitat use. In a wide range of habitats modified by man, such as cities, road networks, hunted or recreational habitats, diurnal species may become nocturnal as a way to avoid human disturbance (Gaynor et al. 2018, Fig. 5). Human development may also lead to changes in species interactions. For example, female pumas (*Puma concolor*) increased their predation rate by 36% in high housing development areas in California as a way to compensate for the decreased time they spent eating on their prey and decreased kill site fidelity (Smith et al. 2015). Species from various taxa have also responded to climate change by modifying their phenology, i.e. the timing of their biological activities or life-cycle events, for example advancing their reproduction because of earlier springs (for examples, see Réale et al. 2003 for North American red squirrels, Both et al. 2004 for laying dates in flycatchers, Gaston et al. 2005 for laying dates in Brunnich's guillemots, Bartomeus et al. 2011 and Leong et al. 2015 for bees, Klaus and Lougheed 2013 for anuran species). Lastly, modifying their physiology may allow species to adapt to changing environments (Wingfield

2008, Wingfield 2015). For example, ectotherms such as the eastern fence lizard (*Sceloporus undulatus*) modulate their thermoregulation in order to avoid heat stress (Buckley et al. 2015). Individuals may also modulate their stress response in order to better cope with global changes (Atwell et al. 2012). For example, dark-eyed juncos (*Junco hyemalis*) living in urban environments have reduced their cortisol excretion and flight initiation distance response when handled by humans, indicating this species might be adapting to its new urban environment without incurring too much damage from an excessive excretion of stress-hormone levels (Martínez-Mota et al. 2007, Angelier and Wingfield 2013). Two specific cases of phenotypic plasticity consist in learning from past experiences and maternal effects (Visser 2008). Maternal effects are the modifications of offspring phenotype due to the maternal phenotype or genotype, and their associated environment and their effects might also mitigate the effects of climate change (Mousseau and Fox 1998, Wolf and Wade 2009). Examples include a copepod species in which maternal effects help to mitigate the effects of a decreased water pH on egg hatching rate (Vehmaa et al. 2012), or the winter moth (*Operophtera brumata*) in which maternal effects may allow to track changes in bud opening timing with climate change (van Asch et al. 2010).

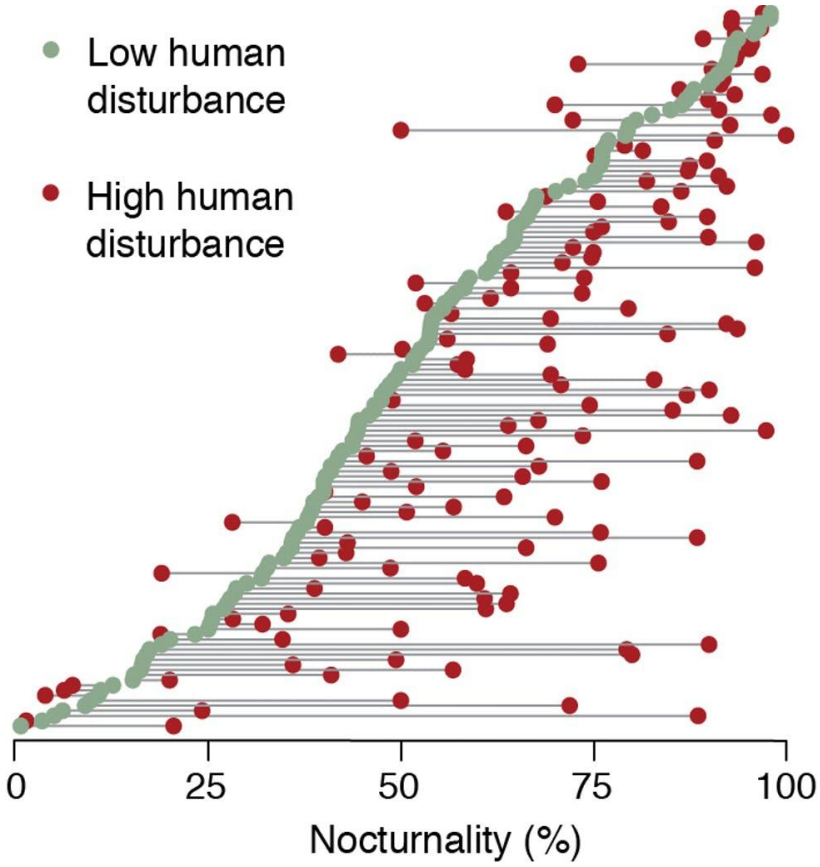


Fig. 5: Paired measures of nocturnality (percentage of activity that occurs in the night) in areas of high human disturbance (Xh) and how human disturbance (Xl), displayed for each species in each study (n = 141 effect sizes, ordered from high to low Xl).The relative change in nocturnality in response to human disturbance was used to calculate the effect size (RR) for the meta-analysis, where RR = ln(Xh/Xl). Figure from Gaynor et al. 2018.

b. Genetic adaptation

Populations may adapt genetically to environmental change through the process of selection of genotypes that maximise fitness, providing that they have enough variability in individual traits (Pulido and Berthold 2004). Indeed, we may expect that natural selection should promote alleles that maximise individual fitness under specific environmental conditions. In a context of global changes, this process could therefore allow populations to adapt and persist by being more adjusted to environmental modifications (Berg et al. 2010). Several examples of this type of adaptation illustrated in scientific research include species reproductive phenology. Studies have for example

suggested that birds have been genetically adapting their reproduction to earlier springs, for example by advancing egg-laying date (Nussey et al. 2005, Visser et al. 2012), although most studies do not have yet fully demonstrated that this change of phenology is due to genetic adaptation (Gienapp et al. 2007, Charmantier and Gienapp 2013). Indeed, egg-laying date has a genetic component, and the variation in that trait may allow individuals to evolve towards earlier egg-laying dates, with a positive impact on lifetime reproductive success. Timing of reproduction has also been advanced in several mammal species, including the red squirrel and the red deer, for which genetic changes have been demonstrated and measured. In red squirrel, earlier parturition date occurred because of increased spring temperatures and food supply and was due to variations in the breeding traits through generations (Réale et al. 2003), while in red deer, authors calculated that evolution was responsible for an advance of ~ 2.1 (95% CI−4.5 to 0.7) days in parturition date in the last four decades (Bonnet et al. 2019). Another example is provided by fruit flies in several continents (Europe, North America and Australia), whose allelic frequencies of physiological genes from northern populations have been shifting towards frequencies found in more southern populations, revealing an adaptation to longer growing seasons (Bradshaw and Holzapfel 2006). Lastly, tropical lizards (*Anolis cristatellus*) have evolved a morphology and behaviour which allow them to better adapt to their new urban range (Winchell et al. 2016).

As previously mentioned, genetic and phenotypic changes are linked and both can contribute to the observed phenotypic changes observed in a species. In the North American red squirrel (*Tamiasciurus hudsonicus*), both genetic and phenotypic changes have been shown to drive species adaptation (Réale et al. 2003). In this species, females have advanced their lifetime parturition date by two weeks in ten years in response to rising spring temperatures and food abundance. The authors have calculated the relative contribution to this modification by both phenotypic plasticity and genetic adaptation and have shown that, although phenotypic plasticity explained most of the observed change in parturition date, microevolution changes also contributed.

2) Dispersal, another way to cope

If individuals cannot adapt to their changing environment, to avoid the associated fitness costs, the only remaining choice is to move away from their current habitat (Berg et al. 2010, Travis and Dytham 2012). A large amount of literature has evidenced distributional shifts in response to climate change, all across the globe, usually poleward or towards elevated regions (Parmesan 2006, Lenoir et al. 2008, Chen et al. 2011, Sunday et al. 2012). Although habitat modifications tend, as a whole, to limit movements such as dispersal (Tucker et al. 2018), similar range shifts have been evidenced in response to habitat modifications, including in the case of human disturbance (ex. Sterck 1998).

a. What is dispersal?

Several movement types may allow individuals to change environments, including migration or nomadism, but the most permanent is dispersal (Singh et al. 2012). Indeed, although previous work used migration and dispersal terms interchangeably in population genetics, migration includes regular (for example, seasonal or diurnal) movements of individuals between different locations, whereas dispersal constitutes a permanent shift away from the natal location (Matthysen 2012). Dispersal is usually defined as the movements of an organism which potentially allow for gene flow (Ronce 2007). It includes natal dispersal, i.e. the movements between the natal place and the site of first reproduction, and breeding dispersal, i.e. the movements between successive reproduction sites (Clobert 2001). While natal dispersal can occur only once in the life of an individual, breeding dispersal may occur several times. This net displacement away from the natal range thus allows individuals to completely change habitats, modifying both their abiotic and biotic environment, which, in the context of environmental changes, may allow them to escape from poor local conditions. Dispersal can be decomposed into three phases: emigration, transfer and settlement (Matthysen 2012). Emigration consists in the departure phase of the individual, which may also contain the exploration or prospecting movements prior to dispersal (Bowler and Benton 2005). The transfer phase is the entire period during which the dispersing individual effectively moves across the

landscape. Settlement occurs when the individuals enter and establish in a new range. Dispersal can either be passive (the dispersing individual is vectored by an abiotic element, such as water or air, by gravity or by an animal) or active (the dispersing individual is mobile and moves by itself).

b. What are the consequences of dispersal?

- At the population level

Dispersal has major consequences on population dynamics and structure (Ronce 2007). At the genetic level, it allows for gene flow between populations, thus limiting inbreeding depression and vehiculing new alleles to potentially isolated populations, which might promote their persistence (Roze & Rousset 2003, 2005). Dispersal also decreases potential genetic drift in the population or mutation load, and for all the aforementioned reasons, dispersal plays an important role in reducing extinction risk in populations. For example, dispersal is considered to play a role in limiting inbreeding depression and genetic drift in the marbled salamanders (*Ambystoma opacum*) (Gamble et al. 2007). However, dispersal may also limit local adaptation: because individuals disperse, they are less likely to bring alleles that are adapted to their settlement range compared to the resident individuals (Lenormand 2002). In terms of population dynamics, dispersal also has a strong effect on the delimitation of species ranges, since it allows individuals to explore and colonise new areas. Moreover, dispersing individuals may also save a population at risk of extinction because of stochastic events, by adding more individuals into that population ("rescue effect", Amarasekare 2004). It also impacts population densities depending on the direction of dispersal flows (Bowler and Benton 2005). Finally, through its important role on species abundance and interactions, dispersal has important implications at the community level (Leibold et al. 2004).

- Benefits at the individual level

At the individual level, dispersal provides the opportunity for individuals to reach novel habitats, potentially of higher quality compared to the area where they were born (Ronce 2007). Novel habitats could benefit individuals at four different levels: the latter may find more resources or

resources of higher quality, more mates or individuals of higher quality, and they may suffer from less disturbance and less risk. Dispersal may also help to alleviate competition between conspecifics by distributing individuals into different habitats (Ronce 2007). In particular, it can provide dispersers with fewer competitors and thus more resources, especially if the density in settlement ranges is lower compared to density in the natal range or if kin competition is pronounced in the natal range (Gyllenberg et al. 2008, Taylor and Buckling 2010). Lastly, changing ranges may also help individuals gain social rank, with better prospects in terms of survival or reproduction (Altwegg et al. 2000).

c. The genetic bases of dispersal

Dispersal has a genetic basis, although the environment contributes to most of the dispersal phenotypes (Saastamoinen et al. 2018). Heritability and experimental evolution analyses both demonstrated the genetic basis of dispersal in a wide range of species, and especially in insects and birds (see Saastamoinen et al. 2018 for a review). Dispersal genetics are highly complex. Indeed, the dispersal process probably involves multiple genes and dispersal may be associated with other traits to form a dispersal syndrome, i.e. a suite of correlated morphological, behavioural and/or life history traits linked with dispersal (Ronce and Clobert 2012, Zera and Brisson 2012, Saastamoinen et al. 2018). Dispersal syndromes may be beneficial for individual fitness, as several traits are expected to covary to increase dispersal success. For example, dispersal is associated with temporal aggressiveness during dispersal in western bluebirds, which increases their colonization success (Duckworth and Badyaev 2007). This genetic basis of dispersal, associated with demonstrated phenotypic variation in dispersal among populations, allows for dispersal evolution, which is particularly interesting in the current context of global changes (IPCC 2014, Ripple et al. 2019). Indeed, it may allow individuals to adopt alternative dispersal tactics, some of which may be selected in a given environmental context, and hence, populations should evolve towards a specific dispersal strategy depending on the environment they encounter (Saastamoinen et al. 2018).

d. Dispersal, a highly heterogeneous process

Dispersal is a highly heterogeneous process, both in its causes and expressions (Fronhofer et al. 2018). Indeed, dispersal is both condition and context-dependent (Bowler and Benton 2005). Firstly proposed for movement ecology, the framework developed by Nathan et al. (2008) also applies to the particular case of dispersal. Within this framework, we usually consider that movements may vary upon four main factors: the **state of the individual**, which might relate to the motivation to move and fulfil some goals – for example, gaining energy (it is related to organism physiology and if applied, psychology), its **motion capacity**, which is the ability to move in the landscape, either by itself for a mobile species (for example, flying in a dispersing bird), or through the use of other abiotic or biotic components in passive dispersal (for example, being carried by water flow for microorganisms), its **navigation capacity**, which is the ability to orientate a dispersal movement in a particular direction depending on the environmental factors perceived by the individual (for example, finding a new pack in social carnivores) and lastly, the **environmental conditions** (biotic and abiotic) incurred by the individual (Nathan et al. 2008). Consistent with this framework, each of these components will act on the three phases of dispersal. Indeed, individuals may adjust their dispersal behaviour plastically in response to environmental cues they perceive and depending on their condition (Matthysen 2012, Fig. 6).

- ❖ Emigration

Emigration signifies leaving its natal range, and thus, familiarity with the environment, the latter being highly beneficial for individuals (e.g. Yoder et al. 2004, Brown et al. 2008). Thus, individuals may base their dispersal decisions on environmental and phenotypic cues which may allow them to decide whether they may benefit more from leaving or staying in their natal range (see Fig. 6).

- ➢ Exogenous factors

Natal habitat quality may have two opposite effects on dispersal. For example, in the African buffalo (*Syncerus caffer*), it might promote dispersal when habitat quality is low, to escape bad environmental conditions, but also in the case of good overall environmental conditions because in

the latter case, individuals are in good body condition, and thus able to offset dispersal costs. Moreover, habitat of high quality may also be of high density (Pettorelli et al. 2001, Spaan et al. 2019), and thus, individuals may disperse to avoid strong intraspecific competition in their native range. Thus, dispersal propensity may vary depending on the species, populations, or even herds (ex. Spaan et al. 2019). Dispersal propensity may also vary with landscape structure, and for instance, decrease with higher levels of habitat fragmentation because chances to reach a settlement habitat become too low (Bonte et al. 2003). Lastly, the biotic environment impacts dispersal propensity, which may for example decrease (Mathieu et al. 2010) or increase (Mayer et al. 2017) with increasing density. Agonistic interactions between residents and juveniles may also increase chances to emigrate (Cant et al. 2001, Aguillon and Duckworth 2015), while other individuals might on the contrary prefer philopatry against dispersal to benefit from their parent (Ronce et al. 1998, Eikenaar et al. 2007). Lastly, individuals may use some cues from immigrant conspecifics which influence their decisions to disperse or not (i.e. informed dispersal, Clobert et al. 2009). These cues may also be used jointly with other factors such as intraspecific or kin competition (Cote and Clobert 2010).

- Endogenous factors

Heterogeneity in dispersal propensity may also come from individual characteristics. First, all sexes and age classes do not disperse in all species. For example in roe deer, only juveniles disperse and in great sharks, only males disperse (Pardini et al. 2001, Debeffe et al. 2012). These differences between phenotypes may be linked to the different selection pressures operating on them (Greenwood 1980, Lawson Handley and Perrin 2007, Martin et al. 2016). Emigration date may also depend on the social rank of an individual, as in Siberian jays (*Perisoreus infaustus*), in which dominant offspring delay dispersal, while sub-dominant offspring disperse as soon as they have reached independence (Gienapp and Merilä 2011). Dispersal also depends on the current capacities an individual has to disperse. Indeed, dispersal is an energy-demanding process (see section III on dispersal costs), and several studies have shown that individuals in good body condition should be better able to perform during and after dispersal than light individuals (Barbraud et al. 2003, Debeffe

et al. 2012, Torrents-Ticó et al. 2018, Searcy et al. 2018). As a consequence, body condition could also be a factor influencing dispersal rates within a population, which has been shown in several species including roe deer (Debeffe et al. 2012, Nunes and Holekamp 1996).

Lastly, environmental cues and phenotype may also interact to influence dispersal propensity: for example, Cote and Clobert (2007) have shown that social personalities may impact the way density influences dispersal in the common lizard (*Lacerta vivipara*). As a consequence, all individuals do not disperse in a population, and dispersal rates are species dependent and both linked to environmental and phenotypic characteristics.

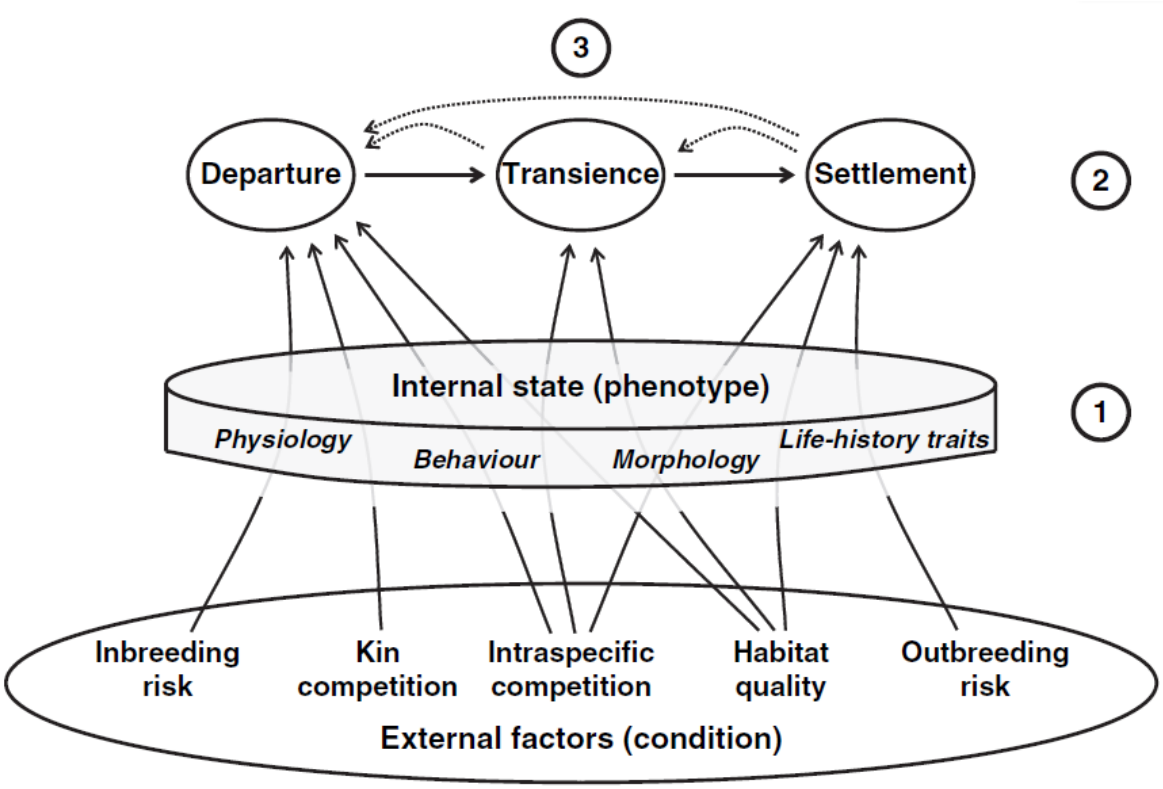


Fig. 6: A conceptual framework to investigate individual variation in dispersal. Relationships between the three dispersal stages (departure, transience and settlement), phenotype-dependent dispersal (i.e. dependence on internal state) and condition-dependent dispersal (i.e. dependence on external factors) are illustrated. We discuss here three main processes shaping individual variation in dispersal: first, phenotypic differences between residents and dispersers should depend on external factors that cause dispersal (1); second, individuals may vary in their sensitivity to conditions encountered during transience and at settlement, given their phenotype and dispersal motivation (2); and third, a transfer of information through individual movements across the landscape might cause unexpected feedbacks between dispersal stages (3, dotted arrows). Figure from Clobert et al. 2009.

❖ Transfer

During transience, individuals should express behaviours that maximise their fitness, and as a consequence, they modify their movement characteristics based on the environment they are experiencing and on their phenotype, including their movement capacities. All characteristics of movement trajectories can be submitted to heterogeneity, including distance, directionality, speed, or frequency of stopovers.

➢ Exogenous factors

First, the transfer phase may be facilitated or impeded by various landscape barriers or corridors, with incidences on dispersal behaviour. For example, landscape structure and composition may restrict the displacements to some areas, for instance if highways or dams prevent individuals to go from one area to another, and thus, influence the potential routes individuals can take during dispersal (Sawyer et al. 2019). Additionally, landscapes may be a source of costs that individuals may try to avoid (see Section III on dispersal costs), such as high mortality risks due to predation or collisions, hunting, etc. (Johnson et al. 2009, Jiguet et al. 2019).Several studies showed that increased fragmentation, which may lead to high mortality risk for dispersing individuals, may lead to straighter dispersal paths (Schtichzelle et al. 2006, Martin and Fahrig 2015). In terms of structure, elements such as forest cover may for example limit dispersal distances in white-tailed deer, probably because forest cover provides the necessary habitat for individuals and they do not have to go further to find a suitable settlement range (*Odocoileus virginianus*) (Long et al. 2005).

Lastly, environments may trigger alternative dispersal tactics, for example in dwarf spiders *Erigone atra,* which can use ballooning or rappelling to disperse, depending on the ambient temperature during ontogeny (Bonte et al. 2008a).

➢ Endogenous factors

Like emigration, heterogeneity in trajectories may also come from individual characteristics. For example, dispersal distance travelled by individuals can also be very variable, within and between

species. Dispersal distance usually increases with the size of species, because large body size is usually associated with enhanced locomotor efficiency, although this might not hold for the largest species, due to locomotory limitations (Stevens et al. 2014). At the species level, both short and long-distance dispersal have been evidenced in the wild (McLellan and Hovey 2001, Linnell et al. 2005, Bonte et al. 2009). Indeed, dispersal distances usually follow a leptokurtic distribution, i.e. the majority of individuals disperse rather short distances, but a few of them disperse long distances, resulting in fat-tailed dispersal kernels (Nathan et al. 2012). Distance may increase for heavier individuals, usually because they have higher dispersal capacities (Debeffe et al. 2012, Wotton and Kelly 2012). Movement patterns may also be influenced by other intrinsic factors, such as behavioural traits or sex (Truvé and Lemel 2003, Valeix et al. 2010, Fig. 6).

- ❖ Settlement
  - ➢ Exogenous factors

Lastly, settlement might also depend on landscape characteristics, for example habitat quality, and social interactions with congeners (Stamps 2006, Rémy et al. 2013, Rehage et al. 2016). Settlement timing may be accelerated when the habitat experienced during transfer is not favourable, or if individuals find a novel habitat containing high-quality resources or mates (Haughland and Larsen 2004). On the contrary, settlement may be delayed or orientated towards unoccupied sites, usually of poorer quality, if dispersers encounter aggressive resident individuals where they intend to settle (Smith 1987). Timing may also vary with the actual movement trajectories an individual is demonstrating. For example, in barn owl, individuals exhibiting more tortuous trajectories usually found their settlement area sooner than those using more straight trajectories (Delgado et al. 2010). Natal habitat also influences the type of settlement habitat dispersers settle in (Davis and Stamps 2004, Benard and McCauley 2008, Stamps 2006). Moreover, it is frequent that individuals settle where they previously explored prior to dispersal (Haughland and Larsen 2004, Selonen and Hanski 2010, Debeffe et al. 2013).

- Endogenous factors

Settlement may also vary with individual factors, including body condition, sex, personality or environmental cues coming from conspecifics. Body condition may also affect the area where individuals settle, with higher body condition individuals settling in richer habitats (i.e. the silver-spoon effect, Stamps 2006, e.g. van Oort and Otter 2005, in black-capped chickadees (*Poecile atricapillus*)). On the contrary, weak individuals may be forced to settle in poor habitats (e.g. in great tits, *Parus major*, Garant et al. 2005). Like emigration, settlement may vary with sex, for example in eagle owls (*Bubo bubo*), where females disperse at longer distances (Delgado et al. 2010). Personality may also affect dispersal. For example, Cote and Clobert (2007) have shown that social personalities may impact the way density influences dispersal in the common lizard (*Lacerta vivipara*). Individuals may also take into account various phenotypic and environmental cues which may influence their dispersal ('informed dispersal', Clobert et al. 2009). For example, in the black-legged kittiwake (*Rissa tridactyla*), individuals use the reproductive success of conspecifics as a cue to decide whether or not to settle in a breeding ground (Boulinier et al. 2008).

As a consequence, dispersal realisation and outcome will depend upon many biological, individual, and environmental factors, leading to variations in terms of propensity to emigrate, timing of emigration, distance travelled, straighter or avoidance of particular areas, settlement success etc. This heterogeneity between individuals may be useful to populations in order to adapt to environmental conditions in the context of global changes.

e. Benefits of dispersal in the context of global changes

There are three main benefits dispersers may obtain by dispersing in the context of global change.

- Escaping deteriorated environmental conditions

Nowadays, many individuals disperse as a way to escape from degraded environmental conditions and reach new habitat patches, and thus dispersal acts as a way to change ranges (Parmesan et al.

1999, Parmesan 2006, Le Galliard et al. 2012). Indeed, publications evidencing species tracking climate change have become common, for example in butterflies, birds and mammals (Warren et al. 2001, Devictor et al. 2008, Schloss et al. 2012). In the context of climate change, some habitats may become inhospitable, while others may be created outside the current range of the species. Dispersal should allow for range shifting and tracking climate change, usually polewards or towards more elevated regions. In the context of habitat fragmentation and degradation by human activities, dispersal also helps colonizing more suitable areas, which should impact the dynamics of the populations (Ronce 2007).

- Rescuing populations from extinction

Global changes currently fragilise populations and potentially lead to increased mortality (Pimm and Raven 2000), which, as a consequence, decreases population sizes. Dramatic losses of individuals have already been demonstrated in a wide range of taxa across the world (Stuart et al. 2004, Thomas et al. 2004, Polidoro et al. 2009). Because dispersal allows new individuals to enter populations, including adding new reproductive mates or helpers in a social species, these could reinforce the endangered populations and help them recover (i.e. rescue effect, Brown and Kodric-Brown 1977). However, this role of dispersal may especially work if efforts are made to decrease the threats responsible for the populations decline, otherwise, the system may work as a source-sink dynamic, whereby dispersing individuals may die in their settlement range, and not allow the population they settled in to recover (Gundersen et al. 2001, Kawecki 2004).

- Maintaining gene flow and connectivity

Whether habitats are lost through human activities or because of climate change, populations could become more and more isolated in the context of global changes, which may increase their risk of extinction, notably because genotypic variation gets reduced (Rieman et al. 1993, Saccheri et al. 1998). In this situation, dispersal also helps maintaining connectivity between remaining patches of habitat, which will impact the genetic structure of the populations. Indeed, several cases of fragmentation showed that genetic diversity was or could be reduced, and that dispersal had a

positive effect on maintaining a sufficient gene flow between populations (Bacles et al. 2006, Dixon et al. 2006, O'Connell et al. 2007). For example, high connectivity was evidenced in a water vole population in Scotland, despite a high level of habitat fragmentation (Lambin et al. 2012). This connected network was constructed through efficient stepping-stone dispersal, allowing dispersers to repeat dispersal movements until they find a suitable area where they can settle, while finding shelter and food between successive movements. The case of stepping stone dispersal thus appears to facilitate individual displacement through a fragmented landscape, as individuals can move long-distances in total, but break them into smaller fractions separated by resting phases (Simberloff et al. 1992, Yang et al. 2016). Lastly, as previously mentioned dispersal has an important role in genetic flow and may increase adaptive potential of populations (Ronce 2007, Garant et al. 2007). Thus, populations may be able to evolve new phenotypes thanks to dispersal which would potentially allow them to cope with global changes, although this effect will depend on the environmental context and evolutionary history (Richardson et al. 2016).

- ❖ Variations in dispersal effects

The degree to which dispersal may be useful in the context of global changes will vary both with the type of environmental change that is occurring, its geographical location and dispersal characteristics. In the case of climate change, the effects dispersal may be more pronounced at the edge margins of the species range, since conditions at these margins might be the first to be impacted by environmental changes (Robinson et al. 2015). Dispersal is also expected to be highly important in trailing ranges, i.e. the contracting range of a population from newly unsuitable habitats (Sheth and Angert 2018), because climate change will make more and more habitats inhospitable in these ranges, which will result in fragmented patches of suitable habitats. In these circumstances, connexions between these habitats, and hence, population persistence, will depend on dispersal.

Dispersal heterogeneity may also have important implications in the context of global changes. All species may not have the same capacities, and thus be able to respond optimally to global change. For instance, the aforementioned example of stepping-stone dispersal might be possible only for

species with a long dispersal lifespan, which is the duration an individual may invest in dispersal compared to other activities. This high dispersal lifespan allows the individual to fragment its dispersal event in several parts and increase the total duration of dispersal, which may not be possible in a species with a dispersal lifespan which cannot be protracted (Lambin et al. 2012). Moreover, because climate is changing at an unprecedented rate, individuals with higher propensities to disperse and longer travelled distances, and thus moving fast through the landscapes, are expected to better track climate change at the expanding front of the species range (Travis 2003, Trakhtenbrot et al. 2005, Travis and Dytham 2012). Long-distance dispersal may also play an important role for future individual fitness in the context of habitat alterations by man. For example, in a population of orange clownfish (*Amphiprion percula*) studied in a network of marine protected areas (MPA) in Papua New Guinea, long-distance dispersers were responsible for up to 10% of the recruitment in adjacent MPAs and thus allowed for populations to remain connected which is fundamental for species conservation (Planes et al. 2009). Long-distance dispersal is also a fundamental component in recovery programs, because species need to rebuild their past range fast in order for the species to persist, and this form of dispersal allows for rapidly expanding a species range while allowing the species to recover a high level of genetic variation (Forbes and Boyd 1997). Moreover, dispersal heterogeneity in terms of strategies involved may also be beneficial for species. For example, the spider *Erigone atra* exhibits two different dispersal strategies depending on the temperature, which allows for the maintenance of the dispersal process even when environmental conditions are modified (Bonte et al. 2008a). However, both strategies do not have the same population consequences, as we will discuss in the third section of this introduction. More generally, better dispersal capacities will also affect gene flow and allele diversity within colonising populations, and thus, species adaptation in its novel environment will be enhanced (Ronce 2007).

III- Costs of dispersal

Although dispersal can have many benefits for dispersing individuals, it also incurs costs during each of the three phases of dispersal, as well as in the pre-emigration and post-immigration periods (Bonte et al. 2012).

1) Four types of dispersal costs

There are four types of costs: risk, time, energy and opportunity costs (Bonte et al. 2012). Most costs may occur at the three phases of dispersal, except for the opportunity costs which occur at the settlement and post-settlement phases (see Fig. 7).

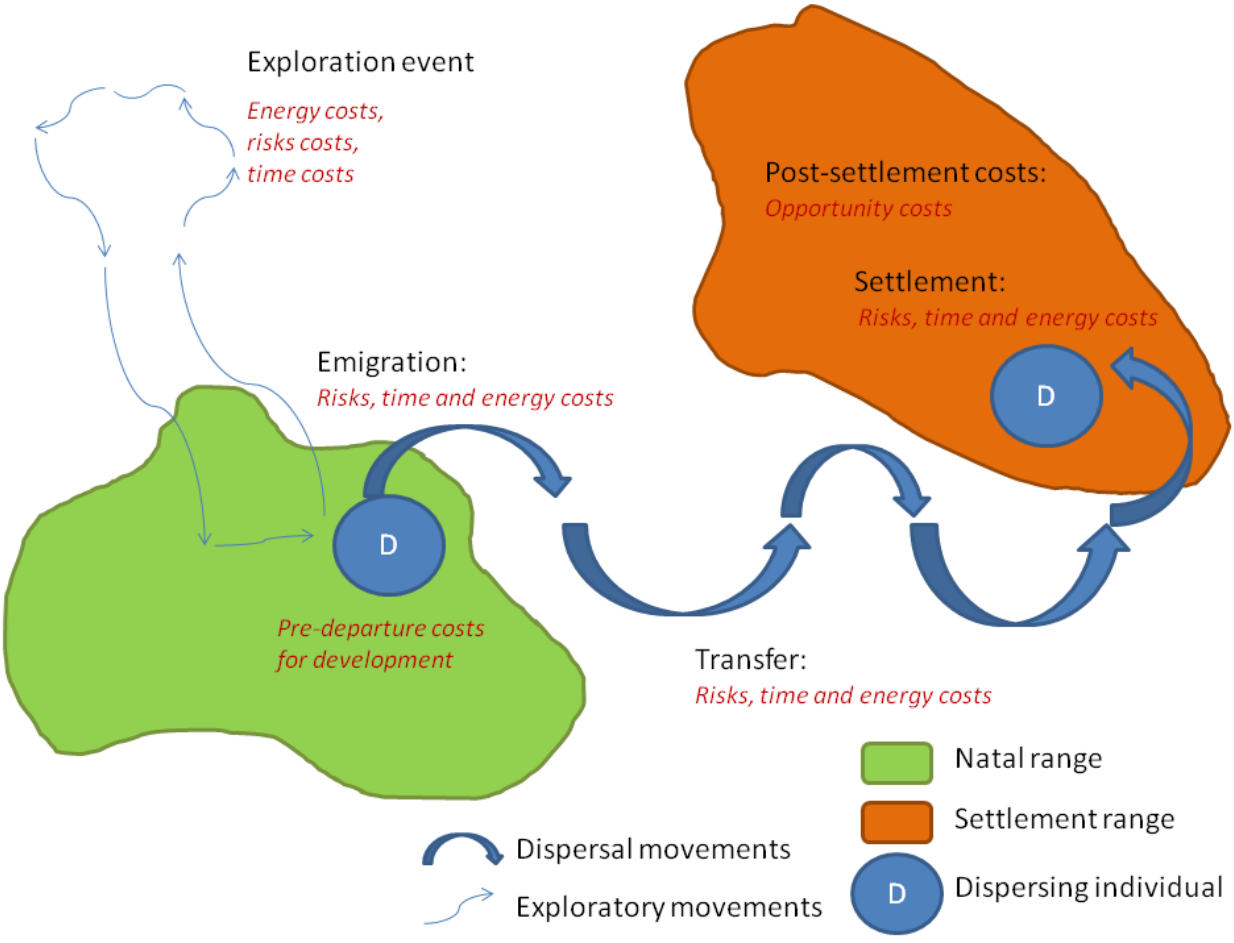


Fig. 7: Figure presenting the possible costs ocurring at each dispersal phase.

a. Risk costs

Risk costs are translated by either direct mortality during dispersal or indirect mortality or attrition, during or outside of the dispersal period. During dispersal, individuals might incur higher predation risks, die from road kills and mortality may occur because of the use of a non-optimal habitat during transience (Alberts and Altmann 1995, Massemin et al. 1998, Ims & Andreassen 2000, Yoder et al. 2004). These mortality risks are thus dependent on the type of environment individuals are experiencing, which may impose various threats, and usually increase when the time spent in this environment increases. For example, American martens (*Martes Americana*) suffer high mortality risks when they disperse for a long distance and if they were born and dispersed within a regenerating landscape, which is of poor quality compared to an uncut landscape, in which survival during dispersal was higher (Johnson et al. 2009). Individuals may also suffer from agonistic interactions with conspecifics, in particular when they try to settle in a new habitat (Griesser et al. 2008, Kahlenberg et al. 2008, Soulsbury et al. 2008). For example, dispersing red foxes (*Vulpes vulpes*) have more wounds compared to their philopatric counterparts, because of the aggressive behaviour of the latter when they try to settle (Soulsbury et al. 2008). Similar behaviours are found in other species, for example rodents (Solomon 2003). Species which passively disperse may be particularly subjected to settlement or post-settlement mortality (Bonte et al. 2012). Indeed, because those species depend on vectors for their dispersal, such as wind, currents, or other species, they are entirely dependent on where these vectors will move them and if the habitat they are carried to is not suitable for their survival, they die (Bonte et al. 2003).

b. Energy costs

Dispersal also implies energy costs, which can be spent either to prepare the organism for dispersal, i.e. developing species specific machinery for dispersal, or as metabolism expenditure during the transfer phase (Bonte et al. 2012). First, individuals might spend energy in order to prepare for dispersal, for example growing wings in order to fly away in the case of aphids, or a shell allowing for

better drifting in a snail (Braendle et al. 2006, Cañete et al. 2007). It is interesting to note that these costs may be paid even by the non-dispersing part of the population, if individuals prepared for dispersal but eventually did not leave their natal range (Bonte et al. 2012). Moving through an unknown landscape requires some energy, which is not going to be allocated to other processes, which might affect body condition. For example, female meerkats that successfully dispersed lost body mass compared to philopatric females (Maag et al. 2019). To counteract this cost, selection has favoured dispersal in individuals which have a good body condition (Barbraud et al. 2003, Debeffe et al. 2012, Searcy et al. 2018, Torrents-Ticó et al. 2018). Other energy costs may include reproductive costs, as dispersers may not be able to reproduce right after dispersal or incur a lower lifetime reproductive success (Braendle et al. 2006, Guerra 2011, Debeffe et al. 2015). Indeed, a trade-off between dispersal and reproduction leads to a negative feedback of dispersal on subsequent reproduction when energy is spent dispersing (Bonte et al. 2012).

c. Time costs

Thirdly, individuals may incur time costs (Bonte et al. 2012). These costs represent a loss of time that individuals may have attributed to other activities such as foraging or resting if they had not dispersed. There are two main consequences of these costs. First, because individuals do not allocate their time to foraging, reproducing or resting when they develop in preparation for dispersal, whether or not they subsequently disperse afterwards or not, their fitness might be reduced (ex: Goodwyn and Fujisaki 2007, Kingma et al. 2016). Secondly, the time spent dispersing may lead to other consecutive costs, such as search costs when trying to settle, which can include direct mortality risks or energy expenditure, or deferred costs, after settlement, which will also affect fitness (Stamps et al. 2005).

d. Opportunity costs

Lastly, opportunity costs arise when individuals settle in a habitat less suitable compared to the one they emigrated from (Bonte et al. 2012). These costs are thus restricted to the settlement or post-settlement phases of dispersal, and come from the loss of advantages individuals had in their natal range either in terms of familiarity with the environment or in terms of favourable environmental characteristics (Yoder et al. 2004, Péron et al. 2010). First, individuals are usually adapted to their natal environment, but may be less adapted to a foreign environment, even if the latter is of good quality, which would necessarily lead to opportunity costs to dispersing individuals (Hereford 2009). Moreover, settling in an inhospitable habitat, which does not provide them with shelter or nutritive requirements, might be particularly detrimental for their body condition and for their fitness (Hansson et al. 2004, Ronce 2007, Pakanen et al. 2016). For example, in the Siberian jays (*Perisoreus infaustus*), dispersers suffer from agonistic interactions with their resident counterparts (juveniles which did not disperse), which do not result in an increase in mortality, but which limit settlement options for dispersers and decrease their reproductive opportunities (Griesser et al. 2008). Indeed, dispersers cannot settle in the high-quality habitats if they are already occupied by aggressive philopatric juveniles, and thus, they have to settle in groups where those juveniles are absent and thus, where reproductive success is lower. Individuals may also lose their social rank or advantages gained through past evolution when they disperse and not gain it back when settling in a new range (Kingma et al. 2016). In the worst situations, dispersal may lead to species maladaptation to their new settlement range. For example, in great reed warblers (*Acrocephalus arundinaceus*), males have a reduced reproductive success because they may be maladapted to their new environment in terms of dispersal characteristics or sing unfamiliar song themes to females (Hansson et al. 2004).

2) Interactions between costs

Dispersal costs should not be considered independently from each other. Indeed, costs may interact at different levels: one cost may lead to other costs, or the combination of costs may jointly impact

the fitness of a dispersing individual. For example, a protracted transience phase may increase time costs, which may in turn lead to increased energy or mortality costs. Energy costs spent during dispersal may also lead to immunodepression, for example in crickets (Adamo et al. 2008). They may also affect direct mortality, as energy depletion prior to dispersal is going to lead to dispersal of energy-deprived individuals. These individuals might have poorer movement capacities because of their bad body condition, and may be less able to escape from predators or survive in general (Barbraud et al. 2003, Torrents-Ticó et al. 2018). High energy costs spent to move through the landscape associated with higher predation risks in the transience habitat may trigger strong attrition costs for dispersing individuals (Yoder et al. 2004).

3) Context and phenotype-dependence of costs

Dispersal costs are both context and phenotype dependent within a given species (Bowler and Benton 2005). Because dispersal is a very demanding process, both in terms of energy spent and risks taken, individuals in good condition may be better prepared to offset the costs associated to dispersal (Barbraud et al. 2003, Torrents-Ticó et al. 2018). As a consequence, dispersal often requires a minimum body condition for individuals to initiate emigration (Nunes and Holekamp 1996, Barbraud et al. 2003, Debeffe et al. 2012, Searcy et al. 2018). Males and females may also not suffer from the same costs. For example, in the Mauritius kestrel (*Falco punctatus*), only females incur fitness costs when dispersing long-distances, by showing a reduced fecundity in early life and a steeper rate of aging in late-life (Nevoux et al. 2013). On the contrary, male Siberian jays (*Perisoreus infaustus*) had lower reproductive success when they dispersed earlier and for longer-distances, which was not the case for females (Gienapp and Merilä 2011). These differences in dispersal costs according to sex may favour the apparition of sex-biased dispersal in some species, along with inbreeding avoidance and asymmetric competition over resources (Greenwood 1980, Gros et al. 2008). Dispersal costs may also vary depending on the type of interactions between dispersers and conspecifics or other species, for example agonistic or non-agonistic interactions (Cote et al. 2010).

For example, Smith and Batzli (2006) showed that dispersing prairie voles (*Microtus ochrogaster*) were more wounded than their philopatric counterparts, because aggressiveness towards unfamiliar voles is high in this species, and led to strong attrition for dispersers trying to settle in a novel habitat.

Dispersal costs are dependent on the dispersal strategy of an individual, i.e. its actual displacement through space, and its environment. As previously mentioned, dispersal costs increase with dispersal distance (Johnson et al. 2009) and the level of straightness of a trajectory may decrease risks costs, as straightness is considered to increase the probability of finding a new habitat patch compared to more tortuous movements (Schtickzelle et al. 2006). Moreover, social dispersal (i.e. moving away from one social unit to another, without necessarily implying changing ranges) and locational dispersal (i.e. geographical range shift, which means the displacement from one area to another) may not have the same consequences, as dispersers are likely to lose many advantages when leaving their kin (Isbell and Van Vuren 1996, Ridley et al. 2008). Dispersal costs are context-dependent, i.e. they vary depending on the environmental characteristics experienced by the dispersing individuals. They are expected to increase if the environment contains high sources of mortality, poor resource quality or abundance or factors preventing individuals from settling, for example high conspecifics competition (Bonte et al. 2012). Dispersal costs also vary with the landscape structure, such as the degree of habitat isolation or crop type, as well as the degree of habitat fragmentation (Russel 2001, Bonte et al. 2003, Cosentino et al. 2011). In particular, dispersing within its preferred habitat may not be as costly as dispersing outside of its natal habitat and crossing an inhospitable landscape (Bonte et al. 2003). Environmental conditions such as temperature or wind velocity may also be responsible for an increase in dispersal costs, potentially in interaction with habitat structure (Bonte et al. 2003, Massot et al. 2008). Indeed, in a fragmented landscape, high wind velocity may displace wind-dispersing individuals outside their suitable habitat, and risks to disperse into an unsuitable habitat should increase with increasing fragmentation (Bonte et al. 2003).

IV- Dispersal evolution in response to global changes

As we previously mentioned, dispersal costs vary with the environment an organism is experiencing and on the organism itself. Thus, in a context of global changes, we expect that these costs will be modified, as well as the benefits (Bonte et al. 2012).

1) Increase in dispersal costs

Mankind is facing a major destruction and modification of natural habitats on the global scale. Because of anthropogenic activities and climate change, many species will lose their natural habitat, and thus, the associated resources they need, including food and shelter (IPCC 2014, Ripple et al. 2019). This loss or degradation of resources should have effects on all types of costs, either directly or indirectly (Bonte et al. 2012) (Fig. 8). First, lack of sufficient resources may have profound effects on body condition and available energy. For example, in common lizards (*Lacerta vivipara*), humidity and temperature play an important role on the abundance of food resources (Massot et al. 2002) and thus, drier environments due to global changes may lead dispersers to cross drier non-optimal environments, where they might incur supplementary costs (Massot et al. 2008). Because dispersal is a costly process, requiring individuals to be in good body condition, we expect that more individuals will choose philopatry over dispersal. This may have important consequences at the population level, because connectivity and gene flow may be reduced. Even if individuals still undertake a dispersal attempt, they may suffer more risks including higher exposure to predators or parasites, compared to if they were in good condition (Murray 2002, Krist et al. 2003, Tucker et al. 2016). Thus, the energy cost of dispersal for individuals in poor body condition may translate into an increased risk cost. A widespread loss of habitat also means that dispersers will have less settlement opportunities. Thus, they will have to search for a place to settle potentially for a long time, and may not be able to find an optimal habitat, leading to both time and opportunity costs (Stamps et al. 2005). Moreover, these

two types of costs may in turn influence body condition and fitness, and thus, may lead to deferred energy and risk costs.

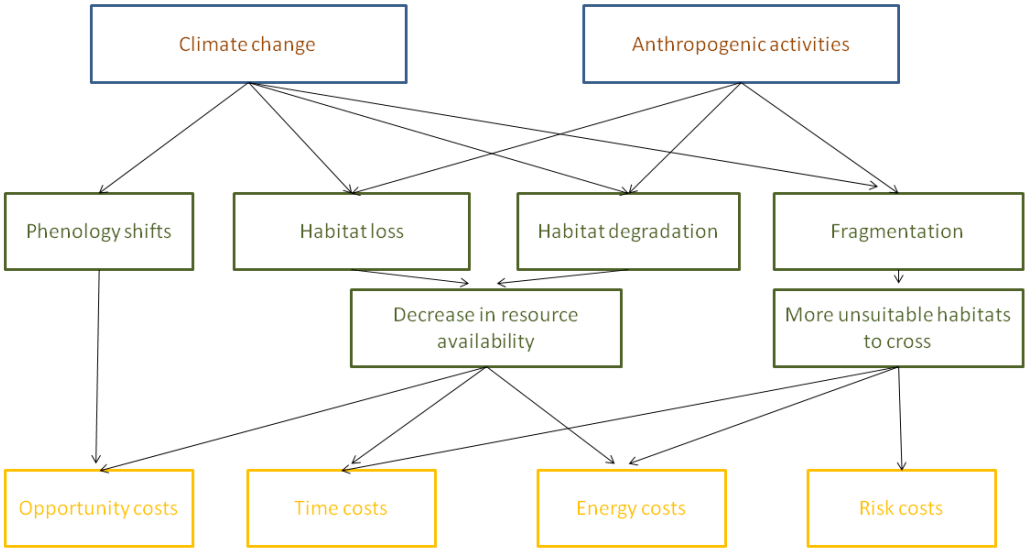


Fig. 8: Possible effects of the two main global changes studied in this PhD, climate change and anthropogenic activities, on the four types of dispersal costs. Anthropogenic activities may be responsible for increased fragmentation or habitat degradation and loss. Fragmentation should lead to more unsuitable habitats (in terms of resources, predators, lack of refuges), which may lead to increased risk, energy and time costs. Habitat loss and degradation should lead to decreased resource availability, which may impact energy, time and opportunity costs. On the other hand, climate change should have an impact on all aforementioned landscape changes (habitat loss, degradation and fragmentation), and consequently, on dispersal costs. It may also lead to phenological shifts in species, which may lead to mismatches between species phonologies, and potential opportunity costs.

Second, global changes are also responsible for a general loss of landscape connectivity (Pringle 2001, Crooks et al. 2011, Senior et al. 2019), which may, for dispersers, translate into increased mortality. Indeed, as suitable habitats are more and more fragmented, individuals will have to cross more inhospitable landscapes to be able to disperse and might incur more mortality risks through increased predation or road-kills (Aars et al. 1999, Bonte et al. 2003, Gardner and Gustafon 2004, Kramer-Schadt et al. 2004, Glista et al. 2007). Moreover, habitat boundary crossing increases mortality because of higher mortality in the matrix compared to within the habitat (Martin and

Fahrig 2015). This higher mortality might increase the level of isolation between habitats. If individuals have to travel longer distances because habitats are not sufficiently connected anymore, they might incur either mortality or reproductive costs (Johnson et al. 2009, Coulon et al. 2010). Moreover, the energetic costs associated with dispersal increase when fragmentation increases, for example as a function of the number of roads crossed (Benoît et al. 2019). Lastly, if landscapes become more fragmented, individuals may have to move for a longer period of time before finding a suitable area where to settle, and thus, they may also incur time and energy costs (Benoît et al. 2019).

Thirdly, climate change may lead to phenological shifts in some species, but not is others (Parmesan 2006). Yet, species are included in a community in which they interact with each other through predation, mutualism, competition, etc. If a species moves from its natural range to track climate change, but the species it depends on does not disperse along with it, or not using the same dispersal decisions, this species may lack previous positive interactions it had in its previous range (i.e. incur opportunity costs) (Berg et al. 2010). For example, insects may disperse farther compared to their plant hosts, which may cause temporal or spatial mismatches and threaten their maintenance in their new habitat (Schweiger et al. 2008, Pelini et al. 2009, Berg et al. 2010, Schweiger et al. 2012). Mismatches may especially be important in the case of specialist species, which require specific conditions to settle and might not be able to adapt in their new range, in comparison to generalist species (Travis 2003, Berg et al. 2010).

Additionally, global changes may lead to shifts in dispersal tactics. For example, high temperature is usually associated with short-distance dispersal (i.e. rappelling) in spiders of the genus *Erigone,* while low temperature is rather associated with long-distance dispersal (i.e. ballooning). Until recently, spiders usually chose ballooning in spring, as temperatures are still rather low at this period, which allowed them to reach high-quality but far habitats for the summer period. However, with climate change, temperatures are rising much earlier in the year, and as a consequence, individuals may

prefer rappelling, which may not allow them reaching habitats with the highest quality. Thus, there may be a mismatch between the strategy chose for dispersing and the quality of resources found in the settlement area (Bonte et al. 2008a) and these spiders may incur more opportunity costs with ongoing climate change.

2) How will dispersal evolve?

Because dispersal evolution is driven by the balance between dispersal costs and benefits and because global changes should exert novel selection pressures on dispersal (Travis et al. 2013, Clobert et al. 2001, Dytham 2009), we expect dispersal to evolve differently in the context of global changes, and that in some cases, dispersal may not be an optimal behaviour anymore (Le Galliard et al. 2012). As a consequence, if dispersal costs outweight the "costs" not to disperse (e.g. inbreeding, competition, etc.), we expect that selection should favour individuals that do not disperse. This should first happen through plasticity in dispersal behaviour, and then, through selection on some dispersal phenotypes.

a. Modifications in behaviours

First, plasticity may be an immediate response to modifications in dispersal costs, and individuals may express varying dispersal behaviours at each of the three dispersal phases. Several studies have already shown that increased dispersal costs and global changes may lead to reduced emigration propensity (Schtickzelle et al. 2006, Massot et al. 2008). Possible causes include increased mortality pressures (Schtickzelle et al. 2006). Individual response may also differ depending on its location within the population (at the core, leading or trailing margins). For exemple, dispersal rates can differ between leading and trailing range margins, which may imply differential connectivities and a global reduction in species ranges, with more global extinctions at the trailing range (Anderson et al. 2009, Philips et al. 2010). Drier environments predicted by climatologists may also lead to a decrease in floods in places, which may reduce dispersal propensity in riverine species adapted to frequent

floods, such as the ground beetle (*Bembidion atrocaeruleum*), in addition to habitat fragmentation (Bates et al. 2006). Decline in dispersal events is a strong concern considering its importance for population dynamics, and might lead to evolutionary traps[1] or suicides[2], and potentially extinctions (Parvinen 2005, Massot et al. 2008, Robertson and Chalfoun 2016). Prior to dispersal, future dispersers may also modify their exploratory behaviour, as has been demonstrated in great tits (*Parus major*): when faced with higher mortality risks, they displayed a more risk-prone behaviour compared to individuals with a lower mortality risk, because it may provide them with potential future mates or resources (Nicolaus et al. 2012). Individuals may also respond plastically to environmental changes by modifying their dispersal trajectories. For example, habitat fragmentation can modify the distances travelled by dispersing individuals or the straightness of their trajectories (Schtickzelle et al. 2006, Van Houtan et al. 2007, Coulon et al. 2010). Lanscape structural modifications by man, such as large open habitats (for example fields), may also constrain the movement directionality (Selonen and Hanski 2004). Similarly, an increase in dessication risks for amphibian species due to climate change may also impact the directionality of dispersal movements, as a way to reach suitable habitats faster (Cosentino et al. 2011). Finally, increasing costs may also reduce selectivity of individuals, i.e. the period during which dispersers are only accepting to settle in a high-quality habitat, so that they settle fast after emigration (Stamps et al. 2005).

b. Evolution

Then, these plastic changes may be selected for depending on the environmental context, and thus can lead to changes in dispersal at the evolutionary level. We can expect that, in the aforementioned examples, some phenotypes leading to a reduction of dispersal propensity or distance may be selected for when fragmentation is high (Schtickzelle et al. 2006, Martin and Fahrig 2015). In other cases, dispersal might still occur, but the process itself may be modified, with the apparition of novel

[1] Evolutionary traps occur when organisms poorly choose their habitats based on cues that correlated formerly with habitat quality but are no longer relevant, Schlaepfer et al. 2002.
[2] As defined by Parvinen (2005), an evolutionary suicide is an "evolutionary process in which a viable population adapts in such a way that it can no longer persist".

phenotypes or even dispersal syndromes (Cote et al. 2017). Dispersal evolution is highly dependent on landscape and phenotypic factors, such as patch size and initial dispersal strategy and species properties (Gros et al. 2006, Kokko and López-Sepulcre 2006), information cues (Bocedi et al. 2012), individual preferences (Bestion et al. 2015), and also interactions between factors, such as combination of landscape and climate changes (Travis 2003, Delattre et al. 2013). These modifications may lead to changes in dispersal strategies. For example, in many systems, more long-distance dispersal events have been shown to evolve in a context of global changes (Hanski et al. 2004, Trakhtenbrot et al. 2005, Moller et al. 2006, Kuparinen et al. 2009). Indeed increasing distance increases dispersal success, because dispersing small distances in a fragmented landscape may lead to settlement in the unsuitable matrix (Mathias et al. 2001). However, as we previously mentioned, increasing dispersal distance may lead to fitness costs (Moller et al. 2006, Coulon et al. 2010). Moreover, although the frequency of long-distance dispersal might increase, in general, the absolute dispersal distance will decrease (Trakhtenbrot et al. 2005). It is important to note that for some species, the effect of fragmentation will directly have a negative effect on dispersal distance: in the northern flying squirrels (*Glaucomys sabrinus griseifrons*), dispersal distance decreases with increased habitat fragmentation, linked with a decrease in the straightness of trajectories, which will also be detrimental for fitness, as inbreeding or competition may arise (Trapp et al. 2019). Thus, in the long term, we can expect selection to act against dispersal (Travis and Dytham 2012). Some species may develop specific alternative dispersal strategies. For example, the dwarf spider *Erigone atra* exhibits two types of dispersal behaviours, rappelling and ballooning (Bonte et al. 2008a). Both allowed individuals to disperse, but rappelling leads to shorter-distance dispersal compared to ballooning. Bonte et al. (2008a) have shown in a context of warming temperatures, rappelling is preferred over ballooning. There are two implications for this behavioural change with temperature. First, population connectivity and gene flow may be reduced, as spiders remain closer to their natal range when rappelling. Moreover, while ballooning allowed individuals to reach crop habitats distributed far from the natal ranges, rappelling may not allow enough individuals to reach crops,

and thus, spiders will not benefit from these rich environments. Thus, if, because of climate change, dispersal evolves towards more rappelling events in this species, which will not be an optimal dispersal strategy for *Erigone atra*, we can expect more deleterious effects on population dynamics and genetics (Bonte et al. 2008a).

3) Aims of the PhD

Although we expect and previous research has shown that global changes can affect dispersal costs, as for now, few studies have actually assessed the direct effects of global changes on dispersal costs, and their consequences for dispersal evolution. More particularly, to this day, we still do not have a precise idea of how dispersal costs will vary with climate change and habitat modifications, and how the dispersal process might evolve. As we previously mentioned, dispersal costs may have impacts in terms of fitness related traits (individual survival and reproduction), but also in terms of dispersal propensity, transfer characteristics, such as dispersal distance, duration, type of trajectory and settlement capacity. All these modifications may in turn affect dispersal evolution, leading to a potentially less dispersive population when costs increase.

In this PhD, I wished to address these gaps, by studying dispersal costs and their effect on dispersal evolution both empirically and theoretically. More precisely, I wished to understand how two of the main causes of extinction, habitat degradation and climate change, may influence dispersal costs, and in turn, dispersal evolution. My general working hypothesis was that global changes may lead to an increase in dispersal costs, including mortality and reproductive costs, at the short, medium and long term, and that, as a consequence, dispersal properties may be modified to the detriment of the dispersal process (including a lower dispersal propensity and decreased global dispersal distances). Moreover, because dispersal costs may vary depending on actual dispersal movement, we first wanted to evaluate the potential dispersal strategies an individual may use. Indeed, many studies have shown marked heterogeneity exists within the dispersal process, suggesting discrete tactics may exist, however, very few studies to our knowledge really demonstrated their existence (but see

Bonte et al. 2008a). Thus, I used three main approaches to test these hypotheses. Because I wanted to address the existence of long-term dispersal costs and different dispersal strategies, I needed data from a species monitored for a long time, and experiencing contrasting environmental conditions that would allow us to test for the effects of environmental variation. I thus used two datasets from two separate roe deer populations in France. The first one is located in Aurignac, in the South of France (Haute-Garonne). This population lives in a highly heterogeneous habitat, containing two main forests, crops, meadows and woodland patches and high human presence (Martin et al. 2018). To demonstrate the existence of alternative dispersal tactics in roe deer in a heterogeneous landscape, I needed precise location data in a mosaic environment. Therefore, I used this GPS-tracked population in Aurignac, which provided me with precise and extensive information on both animal positions and habitat characteristics at each position. The second roe deer population I studied is located in Chizé (Deux-Sèvres). This forest reserve is characterised by two contrasted areas in terms of habitat quality, and has been subjected to increasing droughts and rising temperatures in the last decades (Gaillard et al. 2013). Because I wished to measure the impact of dispersing on survival and reproduction through all steps of an individual's life, in a context of climate change, I needed a long-term longitudinal study. Thus, I used Capture-Mark-Recapture data (CMR) obtained from the roe deer population monitored in Chizé for more than 30 years to address the effects of dispersal on reproduction and survival in a context of climate change. I expected that survival and reproduction may be reduced for dispersing individuals, especially during senescence. Lastly, because dispersal costs are expected to increase with global changes, I expected dispersal traits to be modified in response to global changes. Because generation time is quite long in roe deer (Nilsen et al. 2009), I tested this hypothesis theoretically, using a modelling approach. In particular, I used the software RangeShifter to determine the effects of increasing mortality costs on the evolution of dispersal traits (Bocedi et al. 2014). I expected dispersal to evolve towards shorter and more sinuous trajectories to promote rapid settlement and so mitigate increased dispersal costs.

Model species


Photo by B. Lourtet

To answer my questions, I used the European roe deer (*Capreolus capreolus*) as a model species (Box 1). Indeed, this species is at the core of several main preoccupations in Europe because of its important socio-economic impacts. First, roe deer can cause damage to agricultural or forested areas (Sage et al. 2004); second, it is regularly implicated in vehicle collisions (Bruinderink and Hazebroek 1996, Hothorn et al. 2012); third, it is a disease vector, including for Lyme disease (Vor et al. 2010); and fourth, it is a game species, and thus a source of revenue for rural communities (Burbaiteé and Csanyi 2009).

Roe deer is also a particularly interesting species for the questions I asked in my PhD, because of its unique dispersal event (Debeffe et al. 2012). Female roe deer give birth in spring, usually around May, and at ~8 months old, the young roe deer may undertake a dispersal event, or alternatively, stay philopatric (See Box 2 for more information on roe deer life cycle). Dispersal has been particularly well described in this species (Wahlström and Liberg 1995, Coulon et al. 2006, Gaillard et al. 2008, Van Moorter et al. 2008, Debeffe et al. 2012, 2013, 2014, Vanpé et al. 2016), and thus, allows to use a solid grounding knowledge for this PhD. Moreover, this unique dispersal phase makes roe deer particularly relevant for this study, because it allows determining the precise impact of this life-history event on the entire life-history of individuals.

Lastly, I benefitted from two long-term monitoring programs which provided me with both longitudinal and cross-sectional very high quality data. The first study site is situated in Aurignac (Haute-Garonne), where individuals were tracked using GPS collars since 2002. This area consists in a

heterogeneous landscape densely occupied by human infrastructures (Fig. 9). Crops constitute 36% of the landscape (Martin et al. 2018) and roads are widely spread across the area. Hunting is allowed and drive hunts occur regularly from September to February, while stalking occurs from June to August. The climate is oceanic and temperatures average 11-12°C.

Fig. 9: Aerial view of the Aurignac study site, composed of two main forests and agricultural crops and meadows.

The second study site is situated in Chizé (Deux-Sèvres), where individuals were marked and followed throughout their life in the study area since 1978. Created in 1970, this reserve is an enclosed forest of 2.614 ha managed by the Office National de la Chasse et de la Faune Sauvage (ONCFS). It is composed of oak (*Quercus* sp.) and beech (*Fagus salvatica*), and is divided into two main sectors of contrasting habitat quality for roe deer. Each of these sectors is then subdivided into smaller parcels of ca. 10 ha (Fig. 10). The climate in this area is oceanic with Mediterranean influences, and characterised by mild winters and hot summers. The reserve has been suffering from more frequent droughts in the last 20 years, notably in 2003. Hunting of roe deer is not allowed in the study area and human presence is very low (Pellerin et al. 2017).

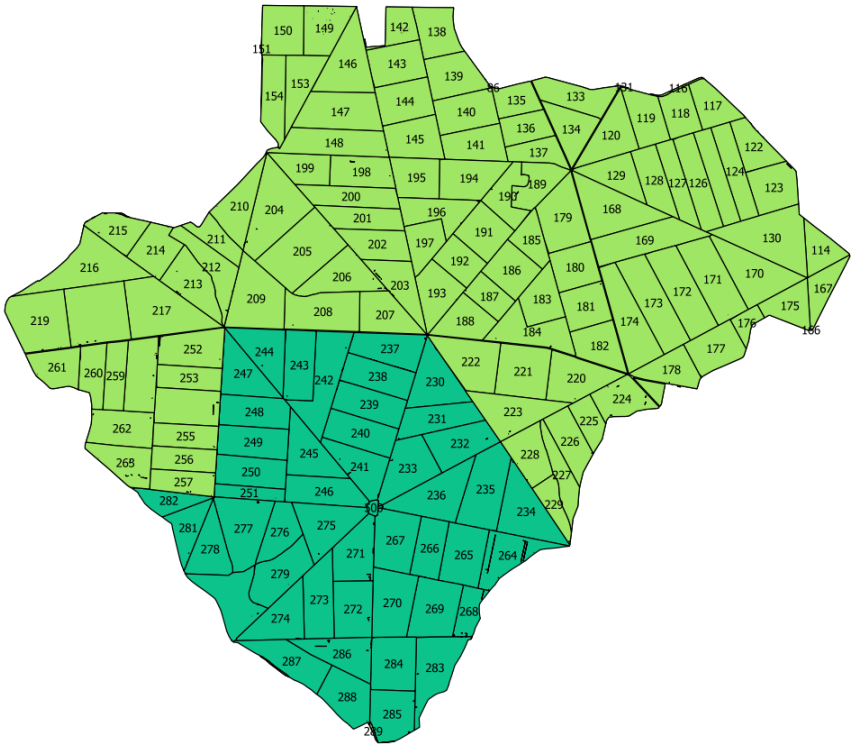


Fig. 10: Map of the Chizé Réserve Biologique Intégrale (RBI). Light green corresponds to the sector of good quality; dark green corresponds to the sector of poor quality. Parcels are delimited with their associated numbers.

Box 1

Roe deer
(*Capreolus capreolus*)

LEAST CONCERN
LC

Order: Artiodactyla
Family: Cervidae


Photo by F. Ribeaudeau

The roe deer is a small cervid found in a large part of Europe, except for many islands including Ireland, Cyprus, Corsica, Sardinia, Sicily.

Most adults weigh between 18 to 49 kg (Andersen et al., 1998) and its body length is usually comprised between 95-135 cm.

Because of its high ecological and behavioural plasticity, roe deer has been able to spread in many diverse habitats, including forests, croplands and meadows. It is now the most abundant species of ungulate in Europe.

Dispersal
⇒ Only at one year old
⇒ About one third of individuals disperse

Fig. 11: Current distributional range or European roe deer - source: Red List of Threatened Species IUCN Version 3.1

Today: 15 000 000 mature individuals estimated

More than 1.5 million in France

Box 2

Roe deer life cycle

In roe deer, fawns are born in spring, between late April and early June (1.). They usually remain with their mother until their first spring (until 9~10 months old). Then, young roe deer can either disperse (2.) from their birth site and settle in a novel settlement range (3.), or stay philopatric , i.e. settle in their natal range. When it occurs, dispersal usually spans from late February to the end of May, with a peak in mid-April.

Females can reproduce as soon as one year old, while males usually start breeding at two years old. The breeding season, also called rut, occurs in summer, between mid-July to mid-August (4.). In this season, males are highly territorial, although the territoriality season usually spans from March to August. Roe deer is a weakly polygynous species and males do not generally mate with more than five females (Liberg et al. 1998).

After mating occurred, the embryo does not immediately start developing: roe deer display embryonic diapause, whereby the fertilised egg does not implant in the uterus until the next winter (usually between December and January, 5.). This delayed implantation may avoid females giving birth during winter. After implantation, gestation usually lasts until roe deer fawns are born in the following spring (usually between the end of April and early June, 6.). Females can have between one and three fawns simultaneously, although they most usually have one or two.

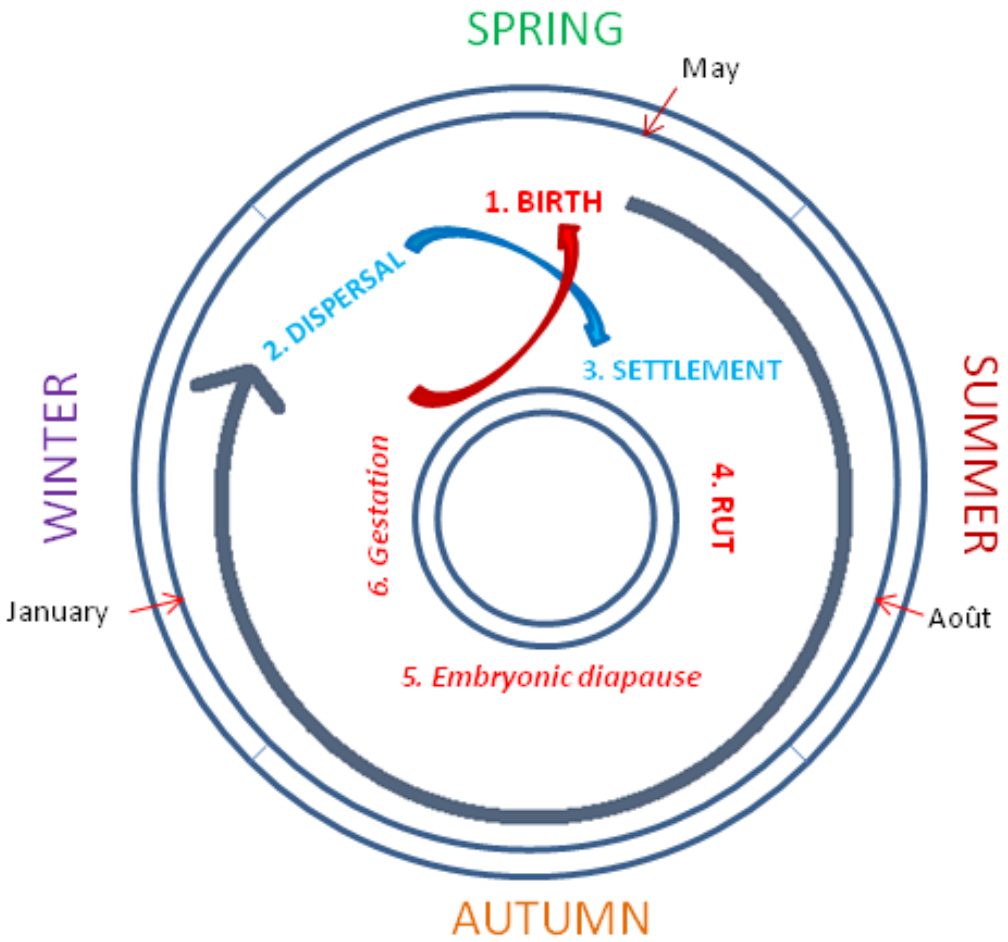


Fig. 12: Roe deer life cycle. In red are mentioned the steps associated with reproduction; in blue are mentioned the steps associated with dispersal

Chapter I:

Climate change increases survival costs of dispersal in roe deer

François Ribeaudeau

Authors : Delphine Ducros[1, 2], Jean-Michel Gaillard[3], Nicolas Morellet[2], Maryline Pellerin[4], A.J Mark Hewison[2], Aurélie Coulon[1, 5]

Affiliations :

1 Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Univ., CP 135, 57 rue Cuvier, FR-75005 Paris, France

2 CEFS, Univ. de Toulouse, INRA, Castanet-Tolosan, France

3 Université de Lyon, Université Lyon 1, UMR CNRS 5558, Villeurbanne Cedex, France

4 Office National de la Chasse et de la Faune Sauvage, Direction de la Recherche et de l'Expertise, Unité Ongulés Sauvages, Gières, France

5 CEFE, CNRS, Univ. Montpellier, EPHE, IRD, Montpellier, France.

Introduction

Dispersal is a fundamental process for population dynamics and persistence, especially in the current context of climate change, because it allows for gene flow, range expansion and population rescue (Ronce 2007). Individuals may respond to climate change by dispersing, which allows them to perform better by tracking their climatic niche (Parmesan 2006, Berg et al. 2010). However, dispersal is also a costly process in terms of mortality risks, energy expenditures, time, and lost opportunities, for example in terms of resources or mates, which might directly impact individual fitness (Clobert et al. 2012). Costs vary with the environmental context an individual is experiencing. In particular, costs are likely to increase in presence of some landscape characteristics (e.g. anthropogenic features, natural barriers) and harsh weather conditions (Bonte et al. 2012) but should decrease with increasing phenotypic quality (condition-dependent dispersal, Bowler & Benton 2005).

Climate change-induced modifications in temperature, precipitation, and wind regimes affect the structure and quality of landscapes. For example, vegetation type and quality are impacted by changing temperatures (Gaillard et al. 2013) and drought intensity increases with climate change (Dai 2011, Trenberth et al. 2014). These changes in habitat quality and structure can decrease the amount

of resources for some species, and thus reduce the amount of energy available for dispersal, leading to energy-deprived dispersers or fewer dispersal attempts (Barbraud et al. 2003). Modifications in resource availability and quality may also increase agonistic interactions towards dispersers in increasingly hostile and resource-limited environments (Grant 1993, Pruetz and Isbell 2000). We thus expect that environmental fluctuations will have clear knock-on effects on dispersal costs (e.g. Bonte et al. 2008, Massot et al. 2008). However, the effect climate change might have on dispersal costs remains unknown, to the best of our knowledge.

The major fitness cost a dispersing individual might incur is mortality (Bonte et al. 2012). Dispersal-induced mortality can be paid at different life stages, either during (direct cost) or after (indirect or deferred cost) dispersal. For example, dispersing individuals might be more exposed to predators or to car collision when dispersing than philopatric individuals (Alberts and Altmann 1995, Massemin et al. 1998). This mortality risk might depend on the degree of familiarity with the landscape travelled, and thereby increase with dispersal distance (Yoder et al. 2004, Johnson et al. 2009). After dispersal, individuals may settle in a poor quality habitat or in an unfamiliar habitat where they might have difficulties in finding food or shelter (Hansson et al. 2004, Ronce 2007, Pakanen et al. 2016), which might be detrimental for their body condition. Individuals might also suffer from agonistic interactions with congeners (Solomon 2003, Soulsbury et al. 2008). As dispersal is energetically costly, dispersing may be detrimental for allocation to other traits, including immune defence, which can lead to increased mortality risk in dispersers (Adamo et al. 2008, Srygley et al. 2009). Trading other traits for dispersing might also have delayed costs. Dispersing quite early in life might have detrimental effects on subsequent life stages, for example in terms of reproduction (e.g. Danchin and Cam 2002, Debeffe et al. 2015), or in late life and increase senescence (Kirkwood and Rose 1991, Bonte et al. 2012, Lemaître et al. 2015). In particular, actuarial senescence, defined as the increase of mortality risk with increasing age, increases when individuals invest early in growth or reproduction in common lizards (Massot et al. 2011). However, although some theoretical work has been done to model the relationship between programmed ages at death and dispersal (Dytham and Travis 2006),

empirical studies of the potential dispersal costs in terms of senescence are, to the best of our knowledge, still lacking.

We aim to fill this knowledge gap by investigating dispersal costs in terms of mortality and actuarial senescence in different ecological contexts. We took benefit of exceptionally detailed data collected on roe deer (*Capreolus capreolus*) population monitored for more than 30 years in Chizé, France, a forest characterised by marked temporal and spatial variation in habitat quality (Pellerin et al. 2010, Gaillard et al. 2013). We expected (i) dispersers to suffer from higher mortality than philopatric individuals, especially at old ages after the onset of actuarial senescence has taken place, (ii) mortality costs of dispersal to be highest when natal and/or settlement habitat quality is poor, (iii) mortality costs of dispersal to increase with climate change, which has previously been shown to negatively impact roe deer survival and reproductive performance (Gaillard et al. 2013), and (iv) dispersal propensity to decrease with climate change because of increasing dispersal mortality costs.

Material and methods

Study site and species

The studied roe deer population inhabits the Chizé Réserve Biologique Intégrale (RBI), an enclosed forest of 2,614 ha located in western France (46°05'N, 0°25'W) that is managed by the Office National de la Chasse et de la Faune Sauvage (ONCFS). The RBI is composed mainly of oak (*Quercus* sp.) and beech (*Fagus salvatica*). The area is divided into two main sectors with contrasted habitat quality for roe deer. The first sector (sector 1) contains mainly oaks with hornbeam (*Carpinus betulus*) and Montpellier maple (*Acer monspessulanum*), and provides abundant resources of good quality to roe deer, whereas the second sector (sector 2) is dominated by beech (Pettorelli et al. 2003) and includes roe deer habitats of low quality. Forest trails further divide the sectors into different parcels of ca. 10 ha. The climate is oceanic with mediterranean influences and the area is characterised by mild winters and dry and hot summers. Monthly temperatures average 5.5°C in winter (January) and 20.5 °C in summer (July), and precitation usually varies between 49 mm and 102

mm (Pettorelli et al. 2003). The area has been suffering from severe drought episodes, especially during the two last decades, which, along with poor soil quality, partly cause the low productivity of this forest (average of 3.77 m^3 of wood produced by hectare and per year, Inventaire National Forestier) (Gaillard et al. 2003, Gaillard et al. 2013). Roe deer density varied between ca. 6.4 (95% CI: 5.4–8.0) and 20.5 (17.1–25.7) roe deer per km^2 in the study period (Pellerin et al. 2017). Roe deer hunting is not allowed, and no large predator is present on the RBI. Public is not authorised to enter the RBI, and thus, human presence is very low (Pellerin et al. 2017).

Roe deer captures

Newborns

From 1985 to 2012, newborns were captured by hand in spring, mostly in May at the peak of births (Delorme et al. 1988). Pregnant females were first localised and tracked, and after birth, the newborn was captured while the mother was away. For each animal, sex and the location of the capture (parcel and sector) were recorded. Individuals were ear-tagged with a unique ID number and, when of known age, marked with a leather collar. Captured roe deer were then released. In total 223 newborns were caught (102 males and 121 females).

Juveniles and adult deer

Our study was based on a extensive survey realised from 1978 onwards in the RBI. Roe deer captures were held in winter for 10 to 12 days in the study area, with people placed regularly along drive nets of 2 to 5 kms and beaters folding individuals towards the net line. About half of the roe deer population present in the forest was captured each year (Gaillard et al. 2003). Once captured, animals were placed in a wooden retention box to prevent stress and injury prior to marking. Juveniles (8-10 months old) were distinguished from older deer based on the presence of a tricuspid third pre-molar milk tooth (Ratcliffe and Mayle 1992). Body mass (kg) and the parcel and sector where the individual had been caught were recorded. If newly caught, individuals are tagged with a

unique ID number using a leather collar and ear tags, and released. Additionnally, from 1982 to 2008, the population was intensively surveyed by field observations between March and December to track the successive locations of each animal (parcel and sector). In total 781 8 months-old roe deer have been caught and tracked from 1982 to 2015, including 390 females and 391 males. Note that some individuals were caught both as newborns and juveniles (46 individuals). From 2012 to 2015, the capture program continued and allowed checking whether roe deer were still alive and their location, but we did not include roe deer born after 2012 to our dataset because these animals were not monitored long enough to become prime-aged adults.

All applicable institutional and/or national guidelines for the care and use of animals were followed. The protocol of capture and blood sampling of roe deer in the Chizé RBI under the authority of the Office National de la Chasse et de la Faune Sauvage (ONCFS) was approved by the Director of Food, Agriculture and Forest (Prefectoral order 2009-14 from Paris). All procedures were approved by the Ethical Committee of Lyon 1 University (project DR2014-09, June 5, 2014).

Discrimination between dispersers and philopatric individuals

By definition, natal dispersal is the process by which an individual leaves its natal area to settle in a new environment where it is likely to reproduce, and thus corresponds to a geographical shift in an individual's range (Ronce 2007). Roe deer disperse only once in their life, at around one year of age, and remain highly faithful to their settlement range afterwards (Hewison et al. 1998, Debeffe et al. 2012). Thus, to classify roe deer into dispersers or philopatric individuals, we measured the overlap between their natal range and their settlement range (i.e. adult range). The natal range of each individual was estimated as the set of parcels where the individual had been captured and observed as a newborn or as a juvenile. In the same way, the settlement range was estimated as the set of parcels where the focal individual had been recaptured and observed from its second summer of life (i.e. after the dispersal period ended) onwards. A roe deer was considered to have dispersed if its

natal and settlement ranges were separated by at least 500 meters (Gaillard et al. 2008). We hence built a 500m buffer zone around the natal range, and measured the overlap between this zone and the settlement range using the functions gBuffer and gIntersection in R (library rgeos, Bivand and Rundel 2017). If ranges were not overlapping, the individual was classified as a disperser; if ranges overlapped, the individual was classified as philopatric. We determined the status of 423 roe deer (the other individuals (N=571) were not recaptured after their first capture as newborn or juvenile and were hence removed from the analyses). All individuals that were translocated to another area or accidentally died by human-related causes (i.e. car collision and problems at capture) were censored after their last capture occasion (N=45).

Period and quality of ranges

As environmental conditions have changed during the last decades in Chizé, which influenced roe deer population dynamics (Gaillard et al. 2013), we assessed the effect of changing conditions in relation to climate change on dispersal costs. We thus divided the study period into three contrasted weather periods. From 1982 to 1993, environmental conditions were overall moderately favourable but variable, with two summer droughts in 1989 and 1990 (Saïd et al. 2005) and a peak of abundance in 1983-1986 that led to density-dependent responses of roe deer performance (Gaillard et al. 1992, 1996). From 1994 to 2002, environmental conditions were highly favourable, with no food limitation and quite low population abundance (Gaillard et al. 2013). Environmental conditions deteriorated from 2003 onwards. The area suffers from increasing temperatures and decreased spring-summer precipitations, including an acute summer drought in 2003 and frequent droughts afterwards (Van Laere et al. 2006, Pellerin et al. 2010). We used roe deer cohort to assign each known-aged individual to one of these three periods and to determine how being born in a given period might have an impact on long-term survival of dispersers.

Because vegetation type has already been shown to have a strong impact on fawn body mass, with potential consequences on their survival (Pettorelli et al. 2003) and dispersal costs are context-

dependent (Bowler and Benton 2005, Bonte et al. 2012), we also characterised habitat quality in natal and settlement ranges as high vs. low, depending on the sector a roe deer lived in, i.e. habitat quality for roe deer living in sector 1 including oaks with hornbeam was higher than habitat quality for roe deer living in sector 2 including beech.

Analyzing the propensity to disperse

To determine whether the proportion of dispersers decreased in the context of climate change and to assess its context-dependence, we analysed the propensity to disperse in relation to period and habitat quality. Because drivers of dispersal are likely sex-dependent (Ducros et al. 2020), we analysed each sex separately. We analysed dispersal propensity as a binary variable and used generalized linear models with a logit link function (library 'stats', < www.r-project.org >). We first built a reference model containing the additive effects of natal and settlement sectors, and period. Then, we compared our reference model with all simpler nested models, including the constant model. We based our model selection on the Akaike's Information Criterion corrected for small sample sizes (AICc, Burnham and Anderson 2002). We first selected the model with the smallest AICc in a ΔAICc of 2 (i.e. the model with the smallest degree of freedom within a ΔAICc of 2). We then removed models within this ΔAICc interval that differed from this higher-ranking model by the addition of one or more parameters, which were considered as uninformative, as recommended by Arnold (2010) and Richards (2008). Then, we performed model averaging on the retained models (library 'MuMIn', Barton and Barton 2019). Additionally, we also analysed the propensity to disperse in relation to sex. We compared a model containing the effect of sex with the constant model, and selected the model with the smallest AICc.

Estimating dispersal costs in terms of survival using Capture-Recapture analyses

We analysed males and females separately because females outlive males in roe deer (Gaillard et al. 1993). We thus built two datasets of capture histories (males: N= 206, females: N=217). In addition

to age, which strongly influences survival of both sexes in roe deer (Gaillard et al. 1993), we considered that the individual dispersal status (two modalities), the study period during which an individual was born (three modalities), and the habitat quality in its natal and settlement ranges (four modalities for dispersers and only two for philopatric roe deer) all potentially influence survival probabilities, either with additive or interactive effects. To allow a more easy interpretation of the influence of the dispersal status on survival, we replicated the analysis per dispersal status (i.e. four datasets corresponding to female dispersers (N=84), male dispersers (N=56), philopatric females (N=133), and philopatric males (N=150)).

Goodness-of-Fits tests

We first performed Goodness-of-Fit tests for single-state data for each of the four datasets to determine the validity of the assumptions of the Cormack-Jolly-Seber model (CJS) that includes full time dependence in both survival and recapture probabilities (Cormack 1964), using the program U-CARE V2.3.4 (Choquet et al. 2009). The violation of these tests suggests the estimation of survival probabilities could be biased, as individuals may not have the same chances to be captured. We used the four main following tests: 3.SR, 3.Sm, 2.CT and 2.CL. The first two tests determine whether all individuals have equal future prospects to be captured, whatever their past history (tests 3). They assess whether individuals newly encountered and previously encountered individuals at a capture occasion i have the same prospect to be reencountered at a subsequent capture occasion i+1 (and thus test the existence of transient indivdiuals, test 3.SR) and if the expected time of reencounter differs between these individuals (test 3.Sm). The two latter tests determine whether individuals have equal future prospects to be captured whether they are currently captured or not (tests 2). They assess whether the probability to reencouter individuals captured at the occasion i at an occasion i+1 is different from the probability to encounter individuals not captured at the occasion i at the occasion i+1 (and thus the existence of trap-dependent individuals, test 2.CT), and if the expected time of reencounter differs between these two categories of individuals (test 2.CL)

individuals. We extracted the p-value associated with each test, and calculated the corresponding over-dispersion parameter, $\hat{c}$, for each of our four datasets.

Survival estimation

After having checked that the CJS model satisfactorily fitted the CR data of each of the four datasets analysed, we estimated survival in relation to period, habitat quality and age using the E-SURGE V2.1.4 software (Choquet et al. 2009). Because in our study all individuals enter the dataset at the fawn or juvenile stage and survive at least until two years old (so that we could determine their dispersal status), the survival probability until two years old was fixed to 1. To account for age-dependent changes in survival, we checked whether the three age-class model (i.e. prime-age adult class from 2 to 8 years old, old adult class from 8 to 13 years of age, and very old adult class from 13 years old onwards) selected from previous analyses (Festa-Bianchet et al. 2003, Gaillard et al. 2013), fitted the data better than a fully age-dependent model. Following previous analysis of the same population (e.g. Gaillard et al. 2013), recapture probability was set to vary over years in each model (i.e. a fully time-dependent capture probability was consistently considered).

We then fitted the most general model containing interactive effects of age classes (that were selected over the full age-dependent model, see Result section), period and habitat quality in natal and settlement ranges. Then we used a step-by-step approach to build successive models, i.e. gradually removing higher order interactions and then main effect of factors of variation from the model (Lebreton et al. 1992). Models were discriminated based on the Quasi Akaike's Information Criterion (QAIC) (Burnham and Anderson 2002), and we selected the model with the smallest QAIC.

Results

1. Analysis of the propensity to disperse

A higher proportion of females dispersed compared to males at all periods (~47% more females than males – see Table S1 and S2 showing the effect of sex on dispersal propensity in the Supplementary Materials). For females, the set of retained models describing the propensity to disperse contained the effect of period and habitat quality in the natal range (Table S3). The propensity of females to disperse decreased from moderate to poor quality periods (estimate of -1.92 ± 0.48 (SE), N=217 – Table S4). The propensity of females to disperse was ~35% lower between periods 1 and 3. Moreover, we found a tendency of females to disperse more if they originated from a poor quality habitat (by ~42%, Table S4). Similarly, the retained model describing male propensity to disperse contained the effect of period, but no effect of natal or settlement habitat quality (Table S5). Male propensity to disperse decreased from moderate to poor quality periods (estimate of -1.14 ± 0.57 (SE), N=206 – Table S6), and the propensity of males to disperse decreased by ~ 38% from period 1 to

2. Goodness-of-fit tests

Three out of the four datasets satisfied the Cormack-Jolly-Seber model's assumptions, the exception being the philopatric males (see Supplementary Materials Annex II) for which the general Goodness-of-Fit test was statistically significant (P = 0.0007). When looking more precisely at the failure of the GOF test, only the 3.SR test was statistically significant (P < 0.0001) and the over-dispersion coefficient was equal to 4.0. A strong age-dependence is likely to account for such a pattern (Lebreton et al. 1992). Considering age effects on survival in our models allowed us to take into account this GOF problem.

3. Survival models

a. Effect of study period, age, and habitat quality on sex- and dispersal type-specific survival

The age-class dependent model accounted for the age dependence of roe deer survival in both sexes for both philopatric individuals and dispersers (Tables S8, S9, S10 and S11). As expected, survival decreased with increasing age (survival of 0.92 (± 0.02), 0.60 (± 0.08), 0.51 (± 0.34) for prime-aged, old, and senescent dispersing males and of 0.86 (± 0.02), 0.60 (± 0.07), 0.48 (± 0.34) for prime-aged, old, and senescent philopatric males, respectively, and of 0.94 (± 0.01), 0.87(± 0.04), 0.61(± 0.08) for prime-aged, old, and senescent dispersing females, and of 0.91 (± 0.88), 0.88 (± 0.76), 0.60 (± 0.37) for prime-aged, old, and senescent philopatric females, respectively). In the following results, we did not study the senescent age class, as individuals surviving after 13 years old are not very numerous, and consequently, the sample sizes for this age class were very small.

In both sexes, the survival pattern of both philopatric and dispersing individuals was best described by the additive effects of age and study period (see Tables 1 to 4). Survival decreased between moderate and favourable quality periods and between favourable and poor quality periods for dispersers (survival of 0.76 (±0.15), 0.50 (±0.10), and 0.36 (±0.09) for moderate, favourable, and low quality periods, respectively, in males; survival of 0.88 (± 0.04), 0.71 (± 0.06), and 0.66 (± 0.08) for moderate, favourable, and low quality periods, respectively, in females). For philopatric roe deer, survival decreased between moderate to favourable quality periods, but tended to increase between favourable and poor quality periods (survival of 0.74 (± 0.14), 0.46 (± 0.10) and 0.51 (± 0.11) for moderate, favourable, and low quality periods, respectively, in males; survival of 0.84 (± 0.06), 0.56 (± 0.06) and 0.62 (± 0.07) for moderate, favourable, and low quality periods, respectively, in females - Fig. 1 and 2). Under the moderate quality period, survival of dispersing and philopatric roe deer was similar for a given age class, whereas in the favourable quality period, dispersers displayed a much higher survival than philopatric roe deer when prime-aged adults, both in males (0.93 ± 0.03 vs. 0.82 ± 0.03) and females (0.93 ± 0.02 vs. 0.86 ± 0.03). In the poor quality period, prime-aged adult survival

was very similar between dispersers and philopatric roe deer in both males (0.82 (± 0.06) vs. 0.86 (± 0.02)) and females (0.91 (± 0.03) vs. 0.91 (± 0.0.02)). However, survival of old dispersers was less than half the survival of old philopatric roe deer in males (0.21 ± 0.06 vs. 0.47 ± 0.10). A similar trend occurred in females, although confidence intervals overlapped and the effect size was much smaller (0.74 ± 0.09 vs. 0.84 ± 0.06).

Table 1: Candidate models describing survival probability of dispersing males including the effect of age classes, three study periods of different environmental conditions, and two habitats of contrasting quality. Models are ranked by order of increasing QAIC; we report the ΔQAIC (difference in QAIC values between a candidate model and the model with the lowest QAIC), the number of estimated parameters (df) and the model deviance. Adult: roe deer from 2 to 8 years old, Old: roe deer from 8 to 13 years old, Very old: roe deer ≥ 13 years old. Natal: habitat quality of natal range; Esta: habitat quality of settlement range. A "." indicates an interaction between two variables and "[ ]" indicates several variables are included in an interaction with another variable. Note that the number of models in this table is superior compared to the number of models for the philopatric males' table (Table 2), as for philopatric individuals, natal and settlement ranges are the same and thus, we only considered one variable for habitat quality. Retained model is highlighted in bold.

Model	Df	Deviance	QAICc	ΔQAICc
Adult + Old + period + Very old	**32**	**481.31**	**558.35**	**0**
Adult + Old + period+ esta + Very old	33	481.23	561.17	2.82
Adult + Old + period + natal + Very old	33	481.27	561.21	2.86
Adult + Old + esta + Very old	31	489.67	563.84	5.49
Adult + Old + period + natal + esta + Very old	34	481.19	564.07	5.72
Adult + Old + natal + esta + Very old	32	489.54	566.58	8.23
Adult + Old + natal + Very old	31	492.65	566.82	8.47
Adult.periode + Old + Very old	31	585.29	659.46	101.11
[Adult+Old].periode+Very old	33	580.12	660.05	101.70
Adult + Old.periode + Very old	31	587.14	661.32	102.97

Table 2: Candidate models describing survival probability of philopatric males including the effect of age classes, three study periods of different environmental conditions, and two habitats of contrasting quality. Models are ranked by order of increasing QAIC; we report the ΔQAIC (difference in QAIC values between a candidate model and the model with the lowest QAIC), the number of estimated parameters (df) and the model deviance. Adult: roe deer from 2 to 8 years old, Old: roe deer from 8 to 13 years old, Very old: roe deer ≥ 13 years old. Natal: habitat quality of natal range; Esta: habitat quality of settlement range. A "." indicates an interaction between two variables and "[ ]" indicates several variables are included in an interaction with another variable. Note that the number of models in this table is inferior compared to the number of models for the male dispersers table (Table 1), as for philopatric individuals, natal and settlement ranges are the same and thus, we only considered one variable for habitat quality. Retained model is highlighted in bold.

Model	Df	Deviance	QAICc	ΔQAICc
Adult + Old + period + Very old	**34**	**1122.64**	**1195.96**	**0**
Adult + Old + period + natal + Very old	35	1122.56	1198.21	2.25
Adult + Old + natal + Very old	33	1137.08	1208.08	12.12
[Adult+Old].period + Very old	35	1358.48	1434.13	238.17
Adult.period + Old + Very old	33	1363.26	1434.27	238.31
Adult + Old.period + Very old	33	1372.92	1443.93	247.97

Table 3: Candidate models of survival probability of dispersing females including the effect of age classes, three study periods of different environmental conditions, and two habitats of contrasting quality. Models are ranked by order of increasing QAIC; we report the ΔQAIC (difference in QAIC values between a candidate model and the model with the lowest QAIC), the number of estimated parameters (df) and the model deviance. Adult: roe deer from 2 to 8 years old, old: roe deer from 8 to 13 years old, Very old: roe deer ≥ 13 years old. Natal: habitat quality of natal range; Esta: habitat quality of settlement range. A "." indicates an interaction between two variables and "[ ]" indicates several variables are included in an interaction with another variable. Note that the number of models in this table is superior compared to the number of models for the philopatric females' table (Table 4), as for philopatric individuals, natal and settlement ranges are the same and thus, we only considered one variable for habitat quality. Retained model is highlighted in bold.

Model	Df	Deviance	QAIC	ΔQAIC
Adult + Old + Very old + period	**36**	**1022.85**	**1094.85**	**0.00**
Adult + Old + Very old + period + natal	37	1022.19	1096.19	1.34
Adult + Old + Very old + period + esta	37	1022.29	1096.29	1.44
Adult + Old + Very old + period + natal + esta	38	1022.15	1098.15	3.30
Adult + Old + Very old + natal	35	1036.11	1106.11	11.26
Adult + Old + Very old + esta	35	1036.76	1106.76	11.91
[Adult + Old].period + Very old	37	1177.69	1251.69	156.84
[Adult + Old + Very old].period	38	1177.67	1253.67	158.82
Adult.period + Old + Very old	35	1185.15	1255.15	160.31
Adult + Old.period + Senescent	35	1190.18	1260.18	165.33

Table 4: Candidate models of survival probability of philopatric females including the effect of age classes, three study periods of different environmental conditions, and two habitats of contrasting quality. Models are ranked by order of increasing QAIC; we report the ΔQAIC (difference in QAIC values between a candidate model and the model with the lowest QAIC), the number of estimated parameters (df) and the model deviance. Adult: roe deer from 2 to 8 years old, old: roe deer from 8 to 13 years old, Very old: roe deer ≥ 13 years old. Natal: habitat quality of natal range; Esta: habitat quality of settlement range. A "." indicates an interaction between two variables and "[ ]" indicates several variables are included in an interaction with another variable. Note that the number of models in this table is inferior compared to the number of models for the female dispersers table (Table 3), as for philopatric individuals, natal and settlement ranges are the same and thus, we only considered one variable for habitat quality. Retained model is highlighted in bold.

Model	Df	Deviance	QAIC	ΔQAIC
Adult + Old + Very old + period	**34**	**1198.67**	**1266.67**	**0**
Adult + Old + Very old + period + natal	35	1198.30	1268.30	1.63
Adult + Old + Very old + natal	33	1216.633	1282.63	15.96
[Adult + Old + Very old].period	35	1414.91	1484.91	218.24
[Adult + Old].period + Very old	35	1415.91	1485.91	219.24
Adult + Old.period + Very old	38	1426.86	1492.86	226.18
Adult.period + Old + Very old	38	1427.75	1493.75	227.08

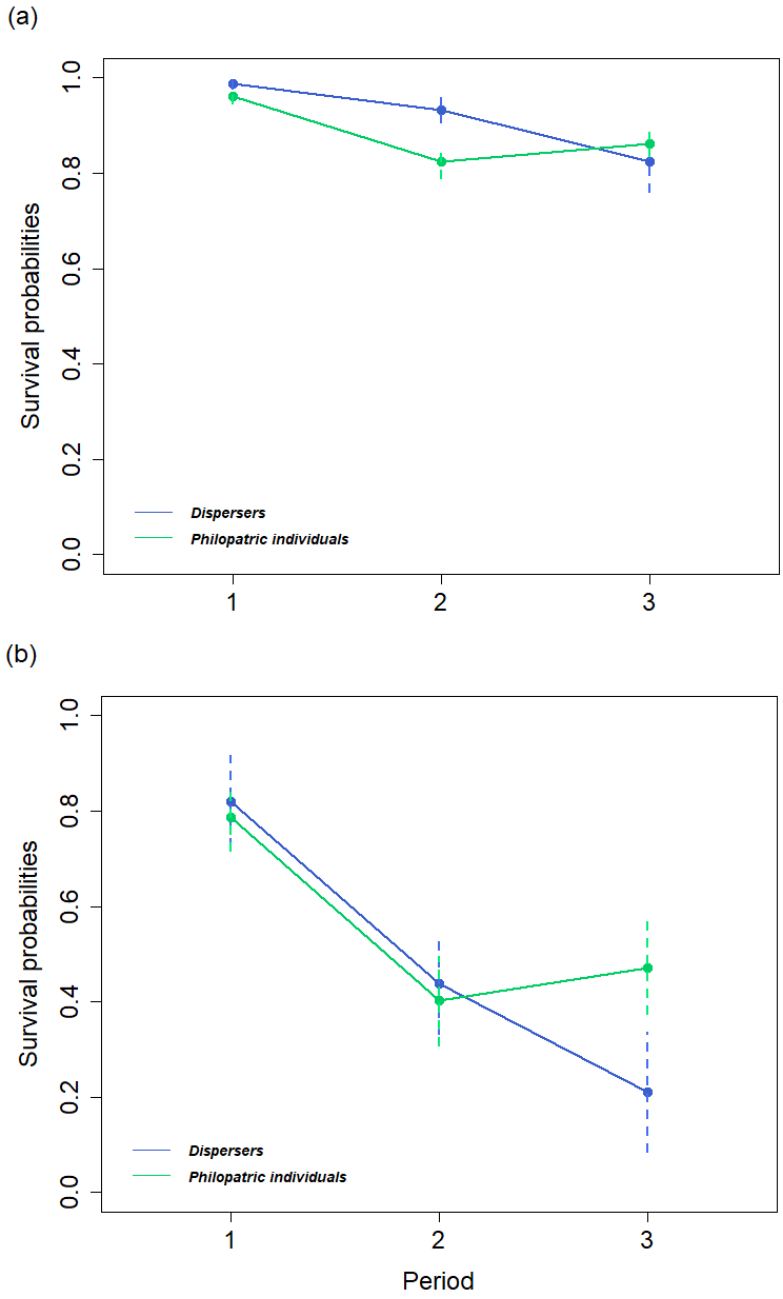


Fig 1. Survival probabilities for dispersing and philopatric males for three study periods with different environmental conditions and two age classes; (a) Adult: 2 to 8 years old and (b) Senescent: from 8 to 13 years old. Period 1 goes from 1982 to 1993, period 2 from 1994 to 2002 and period 3 from 2003 onwards. The dots (and dotted lines) represent the model predictions (and the associated 95% confidence intervals).

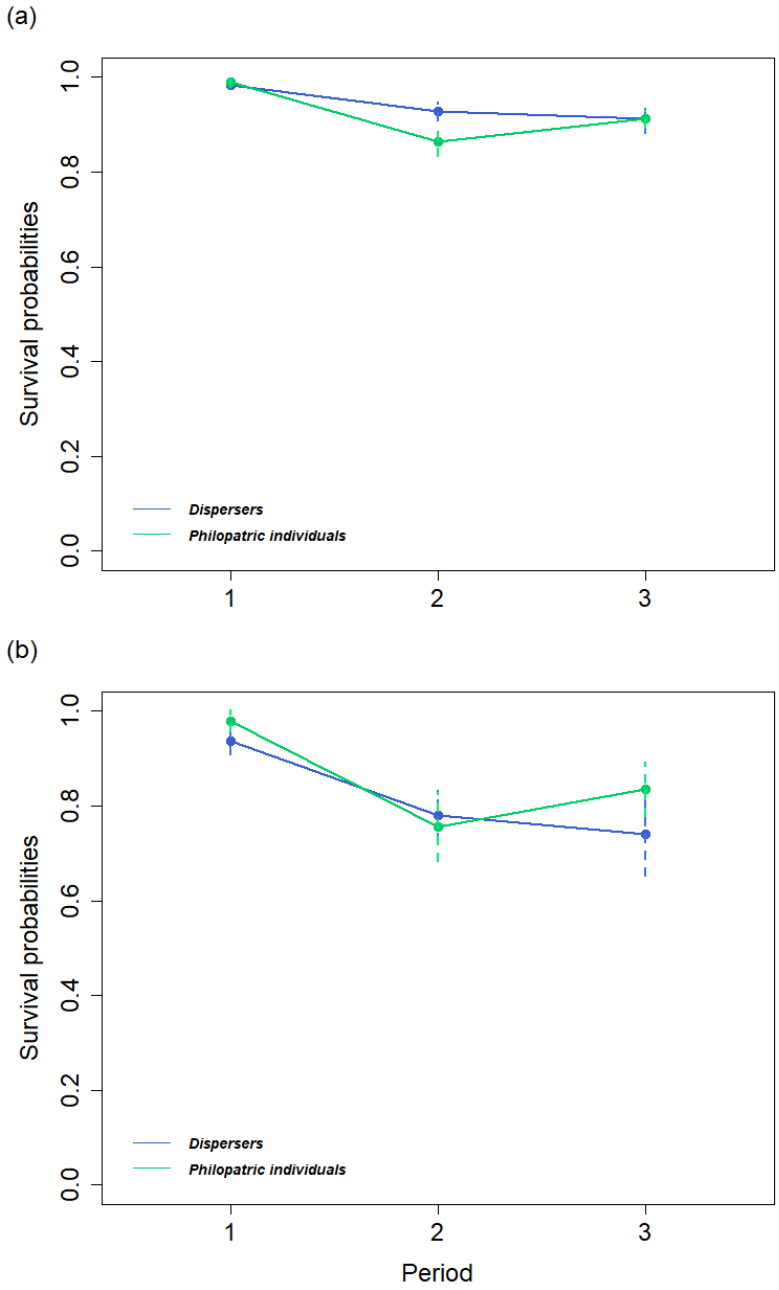


Fig 2. Survival probabilities for dispersing and philopatric females for three periods indexing climate change and three age classes; (a) Adult: 2 to 8 years old and (b) Early senescent: 8 to 12 years old. Period 1 goes from 1982 to 1993, period 2 from 1994 to 2002 and period 3 from 2003 onwards. The dots (and dotted lines) represent the model predictions (and the associated 95% confidence intervals).

d. Effect of habitat quality in natal and settlement ranges

Habitat quality in the natal or settlement ranges, with or without an interactive effect with the period, was never retained in the selected model (Tables 1, 2, 3 and 4). Therefore, we could not detect any effect of habitat quality on long term survival of dispersers and philopatric roe deer of any sex.

Discussion

In this study, we tested whether (1) dispersal was responsible for increased mortality costs in a roe deer population; (2) changes of environmental conditions throughout the study period increased the mortality costs of dispersal and (3) decreased the propensity of individuals to disperse. First, survival probabilities were equal or higher for dispersers compared to philopatric individuals in the first two periods, for both age classes and both sexes, which highlights an effect of individual quality, sensu Wilson and Nussey (2010), with dispersers usually of better quality than their philopatric counterparts. However, since 2003, this trend reversed, with dispersers having an equal or lower survival probability compared to philopatric individuals in both sexes. This increase in dispersal costs may have been responsible for the observed reduction by 2.5 times in dispersal propensity in the last fifteen years, suggesting that the balance between costs and benefits of dispersal might be modified by the deterioration of environmental conditions caused by the global warming, at the expense of the dispersal process. This effect is partially sex-dependent, as female mortality seemed to be less influenced by environmental conditions and dispersed more than males. Lastly, habitat quality did not appear to have a significant impact on dispersal costs, consistently with previous work on this population which showed habitat quality to only influence fawn survival, and at high density only (Pettorelli et al. 2003), although it had a slight effect on the propensity to disperse for females. These results thus suggest that temporal variability may be impacting dispersal costs more than spatial variability, while the latter cannot compensate for the loss of favourable habitats.

High individual quality, defined as consistently high individual performance throughout life, has previously been shown to offset costs of reproduction or movement (Weladji et al. 2008, Hamel et al. 2009, Lescroël et al. 2009, Robert et al. 2012). For example, it is common that individuals of high quality both have a high reproductive success and high survival (e.g. Beauplet et al. 2006, Lescroël et al. 2009, Robert et al. 2012). However, dispersal and individual quality have seldom been linked in studies (but see Cam et al. 2004). Here, when environmental conditions are moderate or favourable, dispersal costs should be rather low, and we suggest that they may be offset by the high phenotypic quality of roe deer dispersers, which allows them to benefit from a high survival both during adult and old adult phases (Wahlström and Liberg 1995, Debeffe et al. 2012). Thus, this study provides further evidence that dispersers are individuals of good quality in this species, and demonstrates that they may completely offset mortality costs in rather favourable environmental conditions. In addition to their high quality, dispersal may allow individuals to reach novel habitats containing high-quality resources, which may confer them additional fitness advantages compared to philopatric individuals.

Climate change is expected to have tremendous impacts on species ecology and should particularly play an important role on resources availability and distribution within landscapes (Backlund et al. 2008, Allen et al. 2010, IPCC 2014). Because roe deer condition is strongly dependent on high quality resources (Hofman 1989, Moser et al. 2006), we expected that changes in resource distribution and quality may increase dispersal costs. We show that, since 2003, senescent dispersers' survival was lower compared to philopatric senescent individuals. This last period of study was characterised by increased temperatures, more frequent droughts and water depletion compared to previous periods (i.e. moderate and then favourable conditions), which led to a global deterioration of the study area (Pellerin et al. 2010, Gaillard et al. 2013). Because of their sensitivity to high quality resources, roe deer attained lower body mass in recent years, and thus, fewer individuals should attain a sufficient body mass to disperse (Debeffe et al. 2012). Moreover, chances to settle in a poor quality environment increased for all individuals but the energy costs the dispersing individuals just incurred were likely harder to offset in an impoverished habitat. These two consequences of environmental

deterioration may have resulted in the observed decrease in dispersal propensity at the population level. Moreover, they demonstrate that dispersers may lose their "reputation" of high quality individuals if environmental conditions become poor, and confirm that dispersal costs may be dependent on current global changes (Bonte et al. 2012).

Sex differences in life history trajectories are widespread in the wild and affect many processes, including dispersal and associated costs (Greenwood 1980, Clutton-Brock 2007, Lawson Handley and Perrin 2007). In mammals, dispersal is usually male-biased, which has also been suggested to be the case for roe deer in past studies, with males dispersing earlier and further than females (Bideau et al. 1993, Wang and Schreiber 2001); however, several recent studies showed that dispersal may not be sex-biased in roe deer (Coulon et al. 2006, Gaillard et al. 2008, Debeffe et al. 2012, Biosa et al. 2015). However, our study both shows higher dispersal costs and a lower dispersal propensity for males, indicating dispersal may be female-biased in this population, consistently with very recent work (Ducros et al. 2020). Because most roe deer male adults are territorial during half the year (Linnell and Andersen 1998) from 3 years of age onwards, dispersing males might suffer from more antagonistic interactions during settlement, especially in a context where resources become scarcer. We suggest that more antagonistic interactions may lead to attrition, increased energy expenditure, and fewer resources acquired (Serrano and Tella 2007, Soulsbury et al. 2008), especially if density of congeners was to increase. This might result in a general decrease in body condition, potentially explaining the stronger senescence we observe in males compared to females. Thus establishing a post-dispersal territory containing aggressive congeners may require a lot of energy in males, especially if they already incur sex-specific costs associated to physiological and behavioural demands for reproduction, which also lead to increased senescence, and especially in a context with poor resources (Douhard et al. 2017). Further work will be required to determine whether dispersing males incur more attrition and body mass loss compared to philopatric individuals, especially in the recent years, while females may not. Moreover, females appear to disperse more compared to males for all periods, contrary to what was previously found in this species (Coulon et al. 2006, Gaillard et

al. 2008). This result also suggests that females may be incurring less costs compared to males, or that costs might be different between sexes or better offsetted by females.

Because declines in life-history traits at old ages are now widespread across a large range of taxa (Ricklefs 2010, Nussey et al. 2013), senescence should influence population dynamics. In a long-lived iteroparous species such as roe deer (Gaillard et al. 2000), reducing survival in old ages might lead to fewer individuals participating to reproduction. Moreover, we also know that individuals born in less favourable periods are of lower quality and usually have a lower reproductive success compared to those born in higher quality years ('cohort effects', Gaillard et al. 2003, Pettorelli et al. 2002). This loss in reproductive individuals or decrease in reproductive success could add up to the effect of climate change on vegetation to explain why recruitment was lower in recent years in this population (Gaillard et al. 2013). In general, changes in senescence patterns might especially be important in the "slow" part of the fast-slow continuum of life-history trajectories, as these species are fitted to an environment triggering low mortality, and thus a mismatch might occur between their "slow" biology cycle and the increased mortality they might be incurring earlier in life (Hassall et al. 2017). Moreover, increasing senescence has been shown to decrease both generation time and population growth rate in mammals, leading to increased extinction risk (Robert et al. 2015). These results might indicate that higher dispersal costs in terms of actuarial senescence may be detrimental for population dynamics, although this effect has to be addressed taking into account other life-history traits such as reproduction and discussing entire life history trajectories.

Dispersal is an energy-demanding process, requiring individuals to be in good body condition to move through an unknown landscape and settle there (Bonte et al. 2012). Because climate change is currently leading to a global deterioration of the study area, with higher mean temperatures and more frequent and intense droughts (Gaillard et al. 2013), we suggest that the observed decline in dispersal is most likely due a climate-induced loss in body condition. In addition to frequent droughts reducing water availability and vegetation quality (IPCC 2007), earlier springs may also impose a

mismatch between the peak in resources and biological processes, including dispersal, and thus create a strong energetic stress on individuals. Previous work on roe deer highlighted that juveniles had to reach a minimum body mass to disperse (Debeffe et al. 2012). Thus, resource-deprived environments may have strong consequences on the body growth of roe deer prior to dispersal and prevent them from dispersing. Observed patterns of body mass variation seem to confirm this hypothesis, as mean body mass decreased in the third period compared to the two previous periods.

Hamilton and May (1977) first predicted that individual dispersal strategies might be age-dependent, and particularly, that dispersal of juveniles may be influenced by their mother's age. Their assumption was verified many years later and research showed that offspring dispersal should decrease when mothers become senescent, and thus when their survival probability decreases (Ronce et al. 1998). Here, the proportion of dispersing individuals in the population decreased in the last period, concomitantly with increased senescence in survival, which could be in line with Hamilton and May's hypothesis. Because actuarial senescence might create spatial heterogeneity in available habitats (Ronce et al. 1998), young roe deer might therefore benefit from staying near their natal range if their parents become senescent, because of the higher probability to inherit from a less crowded habitat, especially in a context where resources might be of poorer quality and quantity. This, however, remains to be evaluated using transgenerational data. Moreover, as we previously mentioned, dispersers also have incurred higher dispersal costs since 2003. If dispersal costs become too high, selection might favour individuals which do not disperse (Travis et al. 1999). In the current context of continuous and increasing climate change (IPCC 2014, Ripple et al. 2019), we might wonder whether both tactics of dispersal and philopatry might persist, or if the current ratio between philopatry and dispersal could be modified. Several studies have already shown that dispersal strategies might vary depending on environmental change (Bonte et al. 2008a, Delattre et al. 2013), and we demonstrate here that dispersal costs may increase with climate change concomitantly with a decrease in the proportion of dispersing individuals. Considering the high implications of dispersal in terms of limiting inbreeding or competition, allowing metapopulations to

persist, or colonizing new habitats (Ronce 2007), modifications of the dispersal process could have far-reaching impacts in biological systems (Bonte et al. 2008a). Thus, we encourage more research on the effects of changing climate on dispersal costs, as a way to better understand how varying environmental conditions might affect population dynamics and assess if we might witness a potential change in movement behavioural tactics in animals.

References

Adamo, S. A., et al. 2008. Competition between immune function and lipid transport for the protein apolipophorin III leads to stress-induced immunosuppression in crickets. – *Journal of Experimental Biology* 211: 531–538.

Alberts, S. C., and Altmann, J. 1995. Balancing costs and opportunities: dispersal in male baboons. – *The American Naturalist* 145: 279–306.

Allen, C. D., et al. 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. – *Forest ecology and management* 259: 660-684.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. – *The Journal of Wildlife Management* 74: 1175-1178.

Backlund, P., et al. 2008. Introduction. In: *The effects of climate change on agriculture, land resources, water resources, and biodiversity*. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research. Washington, DC., USA, 362 pp.

Barbraud, C., et al. 2003. Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. – *J. Anim. Ecol.* 72: 246–257.

Barton, K., and Barton, M. K. 2019. Package 'MuMIn'. R package version, 1(6).

Beauplet, G., et al. 2006. Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. – *Oikos* 112: 430-441.

Berg, M. P., et al. 2010. Adapt or disperse: understanding species persistence in a changing world. – *Global Change Biology* 16: 587–598.

Bideau, E., et al. 1993. Effects of age and sex on space occupation by European roe deer. – *Journal of Mammalogy* 74: 745-751.

Biosa, D., et al. 2015. Do relatives like to stay closer? Spatial organization and genetic relatedness in a mountain roe deer population. – *Journal of Zoology* 296: 30-37.

Bivand, R. and Rundel, C. 2017. rgeos: Interface to Geometry Engine - Open Source ('GEOS'). R package version 0.3-26. https://CRAN.R-project.org/package=rgeos

Bonte, D., et al. 2008a. Thermal conditions during juvenile development affect adult dispersal in a spider. – *Proceedings of the National Academy of Sciences* 105: 17000–17005.

Bonte, D., et al. 2008b. Starvation affects pre-dispersal behaviour of Erigone spiders. – *Basic and Applied Ecology* 9: 308–315.

Bonte, D., et al. 2012. Costs of dispersal. – *Biological Reviews* 87: 290–312.

Bowler, D. E., and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – *Biological Reviews* 80: 205-225.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: A practical information-theoretic approach. – 2nd ed. Springer, New York.

Cam, E., et al. 2004. Assessment of hypotheses about dispersal in a long-lived seabird using multistate capture–recapture models. – *Journal of Animal Ecology* 73: 723-736.

Choquet, R., et al. 2009. U-CARE: Utilities for performing goodness of fit tests and manipulating CApture–REcapture data. – *Ecography* 32: 1071–1074.

Clobert, J. et al. 2012. Dispersal ecology and evolution. – Oxford: Oxford University Press.

Clutton-Brock, T. 2007. Sexual selection in males and females. – *Science* 318: 1882-1885.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. – *Biometrika* 51: 429–438.

Coulon, A., et al. 2005. Dispersal is not female biased in a resource-defence mating ungulate, the European roe deer. – *Proceedings of the Royal Society B: Biological Sciences* 273: 341-348.

Dai, A. 2011. Drought under global warming: a review. – *Wiley Interdisciplinary Reviews: Climate Change* 2: 45–65.

Danchin, E., and Cam, E. 2002. Can non-breeding be a cost of breeding dispersal?. – *Behavioral Ecology and Sociobiology* 51: 153-163.

Debeffe, L. et al. 2012. Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. – *J. Anim. Ecol*. 81: 1327–1327.

Debeffe, L., et al. 2015. Costs of social dispersal in a polygynous mammal. – *Behavioral Ecology* 26: 1476-1485.

Delattre, T., et al. 2013. Interactive effects of landscape and weather on dispersal. – *Oikos* 122: 1576–1585.

Delorme et al. 1988. Interêt de l'étude de la période juvenile pour le suivi de l'évolution d'une population de chevreuils (*Capreolus capreolus*). – *Gibier Faune Sauvage* 5: 15–26.

Douhard, F., et al. 2017. The cost of growing large: costs of post-weaning growth on body mass senescence in a wild mammal. – *Oikos* 126: 1329-1338.

Ducros, D., et al. 2020. Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape. – *Oikos*. 129: 81–92

Dytham, C., and Travis, J.M.J. 2006. Evolving dispersal and age at death. – *Oikos* 113: 530–538.

Festa-Bianchet, M., et al. 2003. Variable age structure and apparent density dependence in survival of adult ungulates. – *Journal of animal ecology* 72: 640-649.

Gaillard, J. M., et al. 1992. Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). – *Canadian Journal of Zoology* 70: 1541-1545.

Gaillard, J.-M., et al. 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. – *Journal of Animal Ecology* 62: 778–791.

Gaillard, J. M., 1997. Early survival in roe deer: causes and consequences of cohort variation in two contrasted populations. – *Oecologia* 112: 502-513.

Gaillard, J. M., et al. 2000. Temporal variation in fitness components and population dynamics of large herbivores. – *Annual Review of ecology and Systematics* 31: 367-393.

Gaillard, J. M., et al. 2002. Cohort effects and deer population dynamics. – *Ecoscience* 10: 412-420.

Gaillard, J. M., et al. 2003. Effects of hurricane Lothar on the population dynamics of European roe deer. – *The Journal of wildlife management* 67: 767–773.

Gaillard, J. M., et al. 2008. Population density and sex do not influence fine-scale natal dispersal in roe deer. – *Proceedings of the Royal Society B: Biological Sciences* 275: 2025–2030.

Gaillard, J. M., et al. 2013. How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. – *Ecology letters* 16: 48–57.

Grant, J. W. 1993. Whether or not to defend? The influence of resource distribution. – *Marine & Freshwater Behaviour & Phy*. 23: 137–153.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. – *Animal behaviour* 28: 1140-1162.

Hamel, S., et al. 2009. Individual variation in reproductive costs of reproduction: high-quality females always do better. – *Journal of Animal Ecology* 78: 143-151.

Hamilton, W. D., and May, R. M. 1977. Dispersal in stable habitats. – *Nature* 269: 578–581.

Hansson, B., et al. 2004. Lifetime fitness of short-and long-distance dispersing great reed warblers. – *Evolution* 58: 2546–2557.

Hassall, C., et al. 2017. Population-level variation in senescence suggests an important role for temperature in an endangered mollusc. – *Journal of Zoology* 301: 32–40.

Hewison, A. J. M. et al. 1998. Social organisation of European roe deer. – In: Andersen, R. et al. (eds.), The European roe deer: the biology of success. Olso: Scandinavian University Press, pp. 189–219.

Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. – *Oecologia* 78: 443-457.

IPCC, 2007: Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson, Eds., Cambridge University Press, Cambridge, UK, 976pp.

IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Johnson, C. A., et al. 2009. Mortality risk increases with natal dispersal distance in American martens. – *Proceedings of the Royal Society B: Biological Sciences* 276: 3361–3367.

Kirkwood, T. B., and Rose, M. R. 1991. Evolution of senescence: late survival sacrificed for reproduction. – *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 332: 15–24.

Lawson Handley, L. J., and Perrin, N. 2007. Advances in our understanding of mammalian sex-biased dispersal. – *Molecular ecology* 16: 1559-1578.

Lebreton J.-D., et al. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. – *Ecol Monogr*. 62: 67–118.

Lemaître, J. F., et al. 2015. Early-late life trade-offs and the evolution of ageing in the wild. – *Proceedings of the Royal Society B: Biological Sciences* 282: 20150209.

Lescroël, A., et al. 2009. Effects of individual quality, reproductive success and environmental variability on survival of a long-lived seabird. – *Journal of Animal Ecology* 78: 798-806.

Linnell, J. D. and Andersen, R. 1998. Territorial fidelity and tenure in roe deer bucks. – *Acta Theriol*. 43: 67–75.

Massemin, S., et al. 1998. Seasonal pattern in age, sex and body condition of Barn Owls Tyto alba killed on motorways. – *Ibis* 140: 70–75.

Massot, M., et al. 2008. Climate warming, dispersal inhibition and extinction risk. – *Global Change Biology* 14: 461-469.

Massot, M., et al. 2011. An integrative study of ageing in a wild population of common lizards. – *Functional Ecology* 25: 848–858.

Moser, B., 2006. Importance of alternative food resources for browsing by roe deer on deciduous trees: the role of food availability and species quality. – *Forest Ecology and Management* 226: 248-255.

Nussey, D. H., et al. 2013. Senescence in natural populations of animals: widespread evidence and its implications for bio-gerontology. – *Ageing research reviews* 12: 214–225.

Pakanen, V. M., et al. 2016. Sex-specific mortality costs of dispersal during the post-settlement stage promote male philopatry in a resident passerine. – *Behavioral ecology and sociobiology* 70: 1727–1733.

Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – *Annu. Rev. Ecol. Evol. Syst.* 37: 637–669.

Pellerin, M., et al. 2010. Habitat use by female western roe deer (*Capreolus capreolus*): influence of resource availability on habitat selection in two contrasting years. – *Canadian Journal of Zoology* 88: 1052–1062.

Pellerin, M., et al. 2017. Saving time and money by using diurnal vehicle counts to monitor roe deer abundance. – *Wildlife Biology* wlb.00274.

Pettorelli, N., et al. 2002. Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. – *Proceedings of the Royal Society of London. Series B: Biological Science* 269: 747-753.

Pettorelli, N., et al. 2003. Spatial variation in springtime food resources influences the winter body mass of roe deer fawns. – *Oecologia* 137: 363–369.

Pruetz, J. D., and Isbell, L. A. 2000. Correlations of food distribution and patch size with agonistic interactions in female vervets (*Chlorocebus aethiops*) and patas monkeys (*Erythrocebus patas*) living in simple habitats. – *Behavioral Ecology and Sociobiology 49:* 38–47.

Ratcliffe, P. R. and Mayle, B. A. 1992. Roe deer biology and management. – London: HMSO.

Richards, S. A. 2008. Dealing with overdispersed count data in applied ecology. – *Journal of Applied Ecology* 45: 218-227.

Ricklefs, R. E. 2010. Insights from comparative analyses of aging in birds and mammals. – *Aging cell* 9: 273–284.

Ripple, W. J., et al. 2019. World scientists' warning of a climate emergency. – *BioScience* biz088

Robert, A., et al. 2012. The interaction between reproductive cost and individual quality is mediated by oceanic conditions in a long-lived bird. – *Ecology* 93: 1944-1952.

Robert, A., et al. 2015. Actuarial senescence can increase the risk of extinction of mammal populations. – *Ecological applications* 25: 116–124.

Ronce, O., et al. 1998. Natal dispersal and senescence. – *Proceedings of the National Academy of Sciences* 95: 600–605.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. – Annu. Rev. Ecol. Evol. Syst. 38: 231–253.

Saïd, S., et al. 2005. Ecological correlates of home-range size in spring–summer for female roe deer (*Capreolus capreolus*) in a deciduous woodland. – *Journal of Zoology* 267: 301–308.

Serrano, D., and Tella, J. L. 2006. The role of despotism and heritability in determining settlement patterns in the colonial lesser kestrel. – *The American Naturalist* 169: E53–E67.

Solomon, N. G. 2003. A reexamination of factors influencing philopatry in rodents. *Journal of Mammalogy* 84: 1182–1197.

Soulsbury, C. D., et al. 2008. Fitness costs of dispersal in red foxes (*Vulpes vulpes*). – *Behavioral Ecology and Sociobiology* 62: 1289–1298.

Srygley, R. B., et al. 2009. Immediate protein dietary effects on movement and the generalised immunocompetence of migrating Mormon crickets *Anabrus simplex* (Orthoptera: Tettigoniidae). – *Ecological Entomology* 34: 663–668.

Travis, J. M., et al. 1999. The evolution of density–dependent dispersal. – *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266: 1837–1842.

Trenberth, K. E., et al. 2014. Global warming and changes in drought. – *Nature Climate Change* 4: 17–22.

Van Laere et al. 2006. Les effets de la canicule de l'été 2003 sur le Chevreuil : Suivi à Chizé. – *Faune Sauvage* 273 : 15–19.

Wahlström, L. K., and Liberg, O. 1995. Patterns of dispersal and seasonal migration in roe deer (*Capreolus capreolus*). – *Journal of Zoology* 235: 455-467.

Wang, M., and Schreiber, A. 2001. The impact of habitat fragmentation and social structure on the population genetics of roe deer (*Capreolus capreolus L.*) in Central Europe. – *Heredity* 86: 703.

Weladji, R. B., et al. 2008. Heterogeneity in individual quality overrides costs of reproduction in female reindeer. – *Oecologia* 156: 237-247.

Wilson, A. J., and Nussey, D. H. 2010. What is individual quality? An evolutionary perspective. – *Trends in Ecology & Evolution* 25: 207-214.

Yoder, J. M., et al. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. – *Behavioral Ecology 15 :* 469–476.

Supplementary Materials

Annex I: Analysis of the propensity to disperse

- Sex model

Table S1: Candidate generalized linear models (glm) describing the propensity to disperse in relation to sex. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
Sex	**2**	**534.70**	**0.00**
Null	1	539.10	4.35

Table S2: Summary statistics of the retained generalized linear model describing the propensity to disperse in relation to sex. We report parameter estimates (±SE) for each variable that featured in the retained models, z values, and p-values. Significant effect is indicated in bold writing.

Parameter	Estimate	Std. Error	z value	P-value
Intercept	-0.460	0.139	-3.297	0.001
Sex Male	**-0.526**	**0.210**	**-2.508**	**0.012**

- Females

Table S3: Candidate generalized linear models (glm) describing the propensity of roe deer females to disperse in relation to three study periods of different environmental conditions, and two habitats of contrasting quality (either in the natal or settlement range). Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). Retained model are highlighted in bold and used for performing model averaging.

Model	df	AICc	ΔAICc
Natal + period	**4**	**262.00**	**0.00**
Period	**3**	**263.70**	**1.78**
Esta + natal + period	5	264.00	2.07
Esta + period	4	265.10	3.19
Natal	2	290.30	28.34
Null	1	291.70	29.73
Esta + natal	3	292.30	30.31
Esta	2	292.90	30.92

Table S4: Summary statistics of the retained generalized linear model describing the propensity of females to disperse in relation to periods of different environmental conditions and two natal habitats of contrasting quality. We report parameter estimates (±SE) for each variable that featured in the retained models, z values, and p-values. Significant effect is indicated in bold writing. The reference period is the period 1 and the reference natal habitat is the high-quality natal habitat.

Parameter	Estimate	Std. Error	Adjusted SE	Pr(>|z|)
(Intercept)	0.504	0.423	0.425	0.236
Natal – poor quality	0.697	0.356	0.358	0.051
Period 2	-0.363	0.481	0.484	0.453
Period 3	**-1.924**	**0.480**	**0.483**	**< 0.001**

- Males

Table S5: Candidate generalized linear models (glm) describing the propensity of roe deer males to disperse in relation to three study periods of different environmental conditions, and two habitats of contrasting quality (either in the natal or settlement range). Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
Period	**3**	**224.90**	**0.00**
Natal + period	4	225.90	1.08
Esta + period	4	226.80	1.95
Natal + esta + period	5	228.00	3.15
Null	1	243.10	18.22
Natal	2	245.10	20.25
Esta	2	245.10	20.26
Natal + esta	3	247.20	22.31

Table S6: Summary statistics of the retained generalized linear model describing the propensity of males to disperse in relation to periods of different environmental conditions. We report parameter estimates (±SE) for each variable that featured in the retained models, z values, and p-values. Significant effect is indicated in bold writing. The reference period is the period 1.

Parameter	Estimate	Std. Error	z value	P-value
Intercept	-0.693	0.500	-1.386	0.166
Period 2	0.464	0.549	0.846	0.398
Period 3	**-1.142**	**0.572**	**-1.996**	**0.046**

Annex II : Goodness-of-Fit Analyses

Goodness-of-Fit tests were realised on each sex:dispersal status group using the software U-CARE V2.3.4 (Choquet et al. 2005, Choquet et al. 2009). In this section, we give the summary statistics associated with these tests.

Table S7: GOF test summary statistics associated to each sex:dispersal status group. The p-value of each model is provided. C-hat represents the ratio between Quadratic Chi2 and df.

Group	p-value	Quadratic Chi2	df	c-hat
Female dispersers	0.84	68.37	81	0.84
Male dispersers	0.99	42.65	69	0.62
Female philopatrics	0.37	90.87	87	1.04
Male philopatrics	0.00065	136.95	88	1.56

Annex III- Age-dependent survival models

In this section, we present the model selection for only age-dependent survival. We tested two different age models: a full-age model and a three age class model (prime-aged adults from 2 to 8 years old, old adults from 8 to 12 years old and very old adults from 12 years old onwards). The four following tables present the results obtained for each of our four sex:dispersal status datasets. Note that, even for identical models, df values may not be identical between the four following tables, because recaptures among the four groups were not equally spread in the study period, and thus, we estimated more or less recapture probabilities for a given year and a given group, leading for more or less degrees of freedom for a given model (for example, in 1982, only males were captured).

Table S8: Candidate models describing survival probability of dispersing males for different age modalities. Models are ranked by order of increasing QAICc; we report the ΔQAICc (difference in QAICc values between a given model and the model with the lowest QAICc), the number of estimated parameters (df) and deviance. Prime-aged adult class: from 2 to 8 years old, Old adult class: from 8 to 13 years old, Very old adult class: >= 13 years old. The retained model is highlighted in bold.

Model	df	Deviance	QAICc	ΔQAICc
Adults + Old + Very old	**29**	**592.64**	**661.18**	**0**
Full-age model	42	574.64	682.40	21.22

Table S9: Candidate model describing philopatric male survival probability for different age modalities. Models are ranked by order of increasing QAICc; we report the ΔQAICc (difference in QAICc values between a given model and the model with the lowest QAICc), the number of estimated parameters (df) and deviance. Prime-aged adult class: from 2 to 8 years old, Old adult class: from 8 to 13 years old, Very old adult class: >= 13 years old. The retained model is highlighted in bold.

Model	df	Deviance	QAICc	ΔQAICc
Adults + Old + Very old	**31**	**1379.87**	**1446.27**	**0**
Full-age model	43	1357.94	1452.58	6.31

Table S10: Candidate model describing dispersing female survival probability for different age modalities. Models are ranked by order of increasing QAICc; we report the ΔQAICc (difference in QAICc values between a given model and the model with the lowest QAICc), the number of estimated parameters (df) and deviance. Prime-aged adult class: from 2 to 8 years old, Old adult class: from 8 to 13 years old, Very old adult class: >= 13 years old. The retained model is highlighted in bold.

Model	df	Deviance	QAIC	ΔQAIC
Adults + Old + Very old	**33**	**1199.21**	**1271.28**	**0**
Full-age model	45	1181.08	1282.64	11.36

Table S11: Candidate model describing philopatric female survival probability for different age modalities. Models are ranked by order of increasing QAICc; we report the ΔQAICc (difference in QAICc values between a given model and the model with the lowest QAICc), the number of estimated parameters (df) and deviance. Prime-aged adult class: from 2 to 8 years old, Old adult class: from 8 to 13 years old, Very old adult class: >= 13 years old. The retained model is highlighted in bold.

Model	df	Deviance	QAIC	ΔQAIC
Adults + Old + Very old	**31**	**1440.02**	**1506.11**	**0**
Full-age	43	1424.42	1518.42	3.02

Chapter II:

Is climate change increasing dispersal costs? A case study on roe deer reproduction and growth

Authors : Delphine Ducros[1,2], Jean-Michel Gaillard[3], Nicolas Morellet[2], Maryline Pellerin[4], Aurélie Coulon[1,5], A.J Mark Hewison[2]

Affiliations :

1 Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Univ., CP 135, 57 rue Cuvier, FR-75005 Paris, France

2 CEFS, Univ. de Toulouse, INRA, Castanet-Tolosan, France

3 Université de Lyon, Université Lyon 1, UMR CNRS 5558, Villeurbanne Cedex, France

4 Office National de la Chasse et de la Faune Sauvage, Direction de la Recherche et de l'Expertise, Unité Ongulés Sauvages, Gières, France

5 CEFE, CNRS, Univ. Montpellier, EPHE, IRD, Montpellier, France.

Introduction

In many taxa, dispersers constitute a non-random part of the population, usually being in very good condition, which allows them to survive dispersal costs and enhance their fitness through dispersal benefits (Barbraud et al. 2003, Bonte et al. 2012). Many studies have already shown that dispersal is usually associated with higher body mass or faster reproductive rates (Clobert et al. 2009, Stevens et al. 2012, Beckman et al. 2018), consistently with the pace-of-life syndrome hypothesis (Réale et al. 2010), although this might not be the case for all species, for example red foxes (Soulsbury et al. 2008, but see Montiglio et al. 2018). According to this hypothesis, dispersers are supposed to be part of the fast component of the fast-slow continuum, exhibiting high growth rate or precocious reproduction (Réale et al. 2010). In these life history strategies, individuals thus incur very strong energy expenditure in early life to realise costly processes such as dispersing, growing and reproducing mainly around the same period in their life (Réale et al. 2010). Early-late life tradeoffs are common in the wild, and individuals investing early in costly processes may suffer subsequent negative consequences throughout their lives (Blomquist 2009, Agrawal et al. 2010, Lemaître et al. 2015, Douhard et al. 2017). Thus, we might expect that individuals realising a dispersing event may

also exhibit high reproductive success and growth in early life at the detriment of their late life reproduction or survival (Réale et al. 2010, Stearns 1989).

In the current context of climate change where resources are becoming scarcer or distributed differently or unpredictably in space and time (IPCC 2014, Ripple et al. 2019), and because tradeoffs are resource-based (Van Noordwijk & Dejong 1986, Agrawal et al. 2010), we may expect the allocation to a given process to be modified (Messina and Slade 1999, Donaldson et al. 2005, Woodhams et al. 2008). Lack of resources may exacerbate an already present trade-off, both in animal and plant kingdoms (Murray and Smith 2012, Vilà-Cabrera et al. 2014). For example, a trade-off exists between thermal safety and resource foraging in the desert woodrat (*Neotoma lepida*): individuals only have limited adaptations for living in an extreme environment (Death Valley, California), and thus, concentrate most of their activity outside the den at night. However, this trade-off has been shown to be exacerbated with increasing temperatures, leading to a stronger negative relationship between woodrat activity and temperature at summer time, which is concerning for population survival and reproduction with ongoing climate change. Thus, changes in tradeoffs with environmental changes, including modifications in, for example, reproduction and growth, may have strong impacts on population dynamics and life history strategies (Stearns 1989).

As for now, there are very few studies which have focused on the effects of climate change on dispersal costs (but see Moller et al. 2006, Bonte et al. 2012). In particular, no study has, to our knowledge, established the joint effects of climate change and dispersal on variations in reproduction or growth throughout an individual's life. In this study, we addressed the potential consequences of climate change on dispersal costs in roe deer (*Capreolus capreolus*) in terms of (1) both male and female growth costs and (2) female reproductive costs. Dispersal occurs only once in the life of roe deer, around the age of one year old, and leads to permanent settlement in a new habitat (Hewison et al. 1998, Debeffe et al. 2012). We hypothesized that this particular movement early in life may have consequences both at medium and long terms (i.e. senescent stage) on

reproduction and growth, and that climate change may modify this interaction. More precisely, we expected that reproductive success and growth might be higher in dispersers in early life compared to philopatric individuals, and that this effect would reverse as individuals get older, according to the pace-of-life syndrome hypothesis. We also expected that climate change may exacerbate the difference in reproductive success and body growth at medium and long terms between dispersing individuals compared to philopatric individuals. Because males and females appear not to have the same weight in roe deer and because associated costs of dispersal may differ between sexes because of differing selection pressures (Pettorelli et al. 2002, Clutton-Brock 2007), we separated analyses by sex. Males are more territorial compared to females in this species (Linnell and Andersen 1998), and thus, they may incur strong energy expenditure or attrition in the settlement phase. Females, on the other side, can reproduce earlier compared to males, at the age of 1 year old, and may thus be incurring high energy expenditures right after dispersing. We expect these two types of energy expenditures to interact with dispersal costs in the trade-offs between dispersal and growth or reproduction, leading to differences in the results obtained for males and females respectively. Thus, we realised analyses separately on males and females.

Material and methods

1) Data

For this second chapter, we used the capture dataset already used in chapter I (Deux-Sèvres, France). Data come from an extensive survey realised from 1982 to 2015 on a roe deer population inhabiting the Chizé Réserve Biologique Intégrale (RBI). Description of the study area and complete capture protocol are described in the material and methods section of this manuscript and in chapter I. For each animal, body mass, sex, and the location of the capture (parcel and sector) were recorded. In females, ultrasonographic measures started in 1983 and allowed to determine whether the female was in gestation, and if so, the number of embryos it carried (between 1 and 3). Subsequent

analyses, as described in chapter I, allowed to discriminate between dispersing and philopatric individuals based on the distance between natal and settlement sectors (disperser: >500m, philopatric individual: <500m; Gaillard et al. 2008). All individuals for which we could not determine the dispersal status were removed from the analysis. Moreover, since we wished to determine the effects of dispersal on subsequent reproduction and body mass, we needed to take into account the condition in which individuals were prior to dispersing. To do so, we used juvenile body mass measured during individuals' first winter because it reflected individual body condition right before dispersal. Thus, we only considered individuals captured as juveniles in winter (and not fawns) in these two analyses. As in chapter I, we considered three contrasted weather periods in this dataset, as environmental conditions have changed in the last decades in the RBI (Gaillard et al. 2013). Periods are described as follows: 1: 1982 to 1993, 2: 1994 to 2002 and 3: from 2003 to 2015. Similarly, we also considered settlement ranges of contrasted habitat quality, depending on the sector a roe deer lived. Settlement sector quality is described as follows: 1: good quality, 3: bad quality. For more details, please see the Material and Methods section of Chapter I.

1) Body growth analyses

We aimed to determine if changes in climatic conditions lead to a lower growth from their juvenile body mass in dispersers compared to philopatric individuals (hypothesis 1), and if this effect differs for different life stages (hypothesis 2). To test our hypotheses, for each sex, we calculated growth (1) all along the individual's life (with the juvenile stage as a reference); (2) for three transitions among stages: from juvenile to yearling, from yearling to adult, and from adult to senescent. Roe deer juveniles realise the majority of their growth during their first year of age (between 59 and 70%, Andersen et al. 1998), and as such, body mass varies strongly in this period. We hence standardised juvenile body mass measures to the median date of capture (27th of January; range = January to February). To do so, we realised a linear regression including the juvenile body mass (at the date of capture) as the dependent variable, the jullian date of capture and sex as independent variables and

year as a random effect on the intercept in order to control for potential year effects (library 'lme4', Bates et al. 2015). This preliminary model allowed us to estimate an average daily body mass gain during the capture period (14.7 ± 2.5 grams.day^{-1}), which we used to calculate a predicted body mass for each juvenile on the 27th of January. Predicted body mass, was calculated in the following way:

Predicted body mass (kg) = Body mass at capture date + daily body mass gain*(median date-capture date)

Growth at a given age was measured as the difference between body mass measured at the corresponding age and the juvenile standardized body mass. We thus obtained multiple measures of growth for each individual, allowing for the comparison of growth between dispersers and philopatric individuals all along their life. Juvenile to yearling growth was measured as the difference between yearling and juvenile body masses. For adult growth, we calculated for each individual the mean adult body mass as the mean body mass measures from 4 to 8 years old in males and from 4 to 12 years old in females (Nussey et al. 2011, Douhard et al. 2017). Adult growth was then calculated by substracting yearling body mass to adult body mass for each individual. We repeated the same method for the senescent stage. This method allowed us to obtain one measure of growth per individual for a given transition.

We first determined the best model describing the age effect on growth, and used it as our base model to evaluate the effects of dispersal status and climate on growth. In roe deer it is known that body mass firstly increases until 4 years of age, where individuals reach their adult mass, stabilizing and then decreasing during a sex-dependent senescent stage at 8 and 12 years old in males and females respectively (Nussey et al. 2011, Douhard et al. 2017). We verified that we found the same variation of growth with age in our population by comparing generalised additive mixed models (gamm, library 'mgcv', Wood 2017) containing either (1) the continuous effect of age, (2) age classes (4 to 8 years old: adult and >8 years old: senescent for males and 4 to 12 years old: adult and >12

years old: senescent for females), (3) age modelled using a threshold effect at ages from 8 to 12 years old or (4) age modelled using a thin plate regression spline. Individual identity and cohort were included as random effects on the intercept in order to account for the lack of independence between measurements and to control for potential cohort effects (Gaillard et al. 2003, Van de Pol and Verhulst 2006). After selecting the best model (see model selection below), we evaluated whether the effect of age varied with dispersal status. We used the retained model for subsequent analyses.

To evaluate the hypothesis 1, we then used gamm models to investigate the variations in growth, which included the three way-interaction between dispersal status, period and juvenile body mass, in addition to the retained effect of age and the effect of settlement sector quality. Adult body mass depends on juvenile body mass in many species including ungulates (Festa-Bianchet et al. 2000, Michel et al. 2015), and thus, we included it in every model we ran to control for its effect on growth. We compared this reference model to simpler nested models which matched biologically meaningful hypotheses and could contain a combination of dispersal status, body mass, period, sector quality and interactions between all these variables but sector quality (see full list of evaluated models in model selection tables in the Supplementary Materials). Two individuals were removed from the analysis because their information seemed erroneous (one had an extremely low juvenile body mass and the other presented a loss of body mass at the yearling phase while it was in very good condition both before and after this phase.

To evaluate hypothesis 2, we built three models, explaining growth from juvenile to yearling, from yearling to adult, and from adult to senescent. In these analyses, models contained the three-way interaction between juvenile body mass, dispersal status and period, the additive effect of settlement sector quality and the cohort included as a random effect on the intercept. We proceeded to the same model selection procedure as explained above.

We based our model selection using the Akaike's information criterion corrected for small sample size (AICc, Burnham and Anderson 2002). We first selected the model with the smallest AICc in a

ΔAICc of 2 (i.e. the model with the smallest degree of freedom within a ΔAICc of 2). We then removed models within this ΔAICc interval that differed from this higher-ranking model by the addition of one or more parameters. These models were considered as uninformative, as recommended by Arnold (2010) and Richards (2008) and removed. Then, we performed model averaging on the retained models (library 'MuMIn', Barton 2019). In the case when only one model needed to be chosen (for example to determine the effect of age), we kept the model with the smallest AICc.

2) Reproductive success analyses

Our aim was to test three hypotheses: when climate is degrading, (1) dispersing females reproduce less compared to philopatric ones throughout their lives, (2) age of primiparity is delayed because of dispersal, and (3) the number of embryos is lower for dispersing compared to philopatric females both shortly after dispersal (i.e. at one year old) and in the entire life of the individual. To evaluate our hypotheses, we estimated the probability to reproduce (P_{rep}) and the probability to get more than one embryo (P_{emb}), which we both considered during the entire life of the individual to determine the whole possible costs that may arise from dispersing (P_{rep_tot} and P_{emb_tot}) or at 2 years old to determine the short-term effects of dispersal on reproduction (P_{rep2} and P_{emb2}). Both variables were obtained by the echography measures. P_{rep} was set to 1 if females were found pregnant, otherwise, P_{rep} was set to 0. P_{emb} was set to the number of embryos detected by echography, and took values from 0 to 3 in our dataset. Because the number of females having 3 embryos was very low (N=2), we gathered females having 2 or 3 embryos as females having more than one embryo and compared them to those having one embryo only. Both variables hence followed a binomial distribution.

Similarly as for the growth analyses, we first determined how these two metrics varied with age, modelling it in four different ways (continuous effect, age classes, smoothed or threshold effect), and whether the effect of age varied with dispersal status (for P_{emb_tot} and P_{rep_tot}). The model also

included the identity of the individual and cohort as random effects on the intercept. We used generalised additive mixed models (gamms) to compare these four types of models. If the smoothed effect of age was included in the retained model, we used gamm models for subsequent analyses. Otherwise, we used a generalized linear mixed model, using the library 'lme4' (Bates et al. 2015).

The complete models were then based on these retained age models (one for each of the four response variables), by adding the interactive effects of dispersal status and period and the additive effect of settlement sector – except for the models investigating short term effects of dispersal (P_{rep2} and P_{emb2}), for which the effects of age and identity were not relevant. We then used glmer models to study the variations of these two variables at 2 years old (library 'lme4', Bates et al. 2015). We used the same model selection procedures as for the growth analyses.

Results

I- Growth analysis

1) Variations of growth in males

a. Variations of growth throughout the entire life

Results showed that male growth varied non-linearly with age, and that this effect was not modified by dispersal status (Supplementary Materials Annex I, 1) and 2)). We thus modelled the age effect using a thin plate regression spline which was not specific to dispersal status in the following models. The best model describing male growth contained the interaction between period and juvenile body mass in addition with the smoothed effect of age (all but one models within a ΔAICc of 2) (Table S3). As expected, male growth increased with age until 4 years old, stabilised up until 8 years old and decreased after 8 years old (Fig. 1, Table 1). The model indicated a negative relationship between male growth and juvenile body mass in both periods 2 and 3 (Fig. 2), indicating individuals gained less

weight if they were heavy as juveniles than light individuals. However, in period 3, the slope between male growth and juvenile body mass was about 2.5 times more pronounced compared to period 2 (estimate of the two-fold interaction of 0.29 ± 0.12 (SE) compared to period 2, N=181, Table 1 and Fig. 1), indicating that individuals might gain between 20 and 30% less weight from a given juvenile body mass if they were born in period 3 compared to period 2 and especially if they were light as juveniles (between 10 and 15 kg).

Table 1: Summary statistics of the retained generalized additive mixed model describing male growth from juvenile stage across an individual's life in relation to age, body mass and period. We report parameter estimates (±SE) for each variable that featured in the retained models, t values, and p-value. For smooth effects, we give the effective degrees of freedom (edf), the residual degree of freedom (Ref.df), the Wald Statistic (Chi.sq) and the p-value. Significant effects are indicated in bold writing.

Parameters	Estimate	Std. Error (SE)	t value	Pr(>|t|)
(Intercept)	15.56	1.46	10.64	< 0.001
Body mass	-0.46	0.08	-5.52	< 0.001
Period 1	-6.79	4.46	-1.52	0.13
Period 3	-6.11	1.93	-3.17	0.002
Body mass:period 1	0.45	0.27	1.68	0.09
Body mass:period 3	**0.29**	**0.12**	**2.33**	**0.02**
Smooth effects :				
	edf	Ref.df	Chi.sq	p-value
Random effect of cohort	**12.95**	**24**	**16.67**	**0.003**
Random effect of individual Identity	**109.99**	**174**	**3.51**	**< 0.001**
s(Age)	**5.98**	**6.99**	**31.99**	**< 0.001**

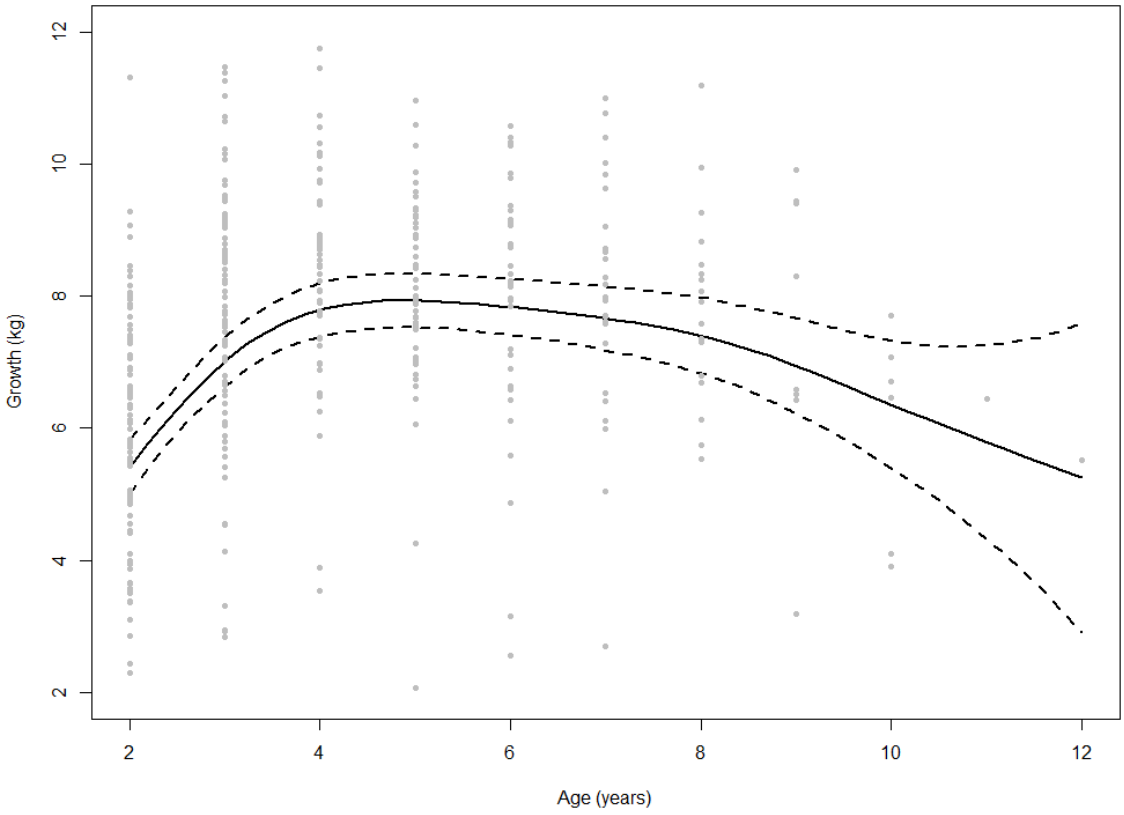


Figure 1: Variations in male growth (kg) from the juvenile stage in relation to age. The line (and dotted lines) represents the model predictions (and the associated 95% confidence intervals). Points represent the observed growth values for a given age.

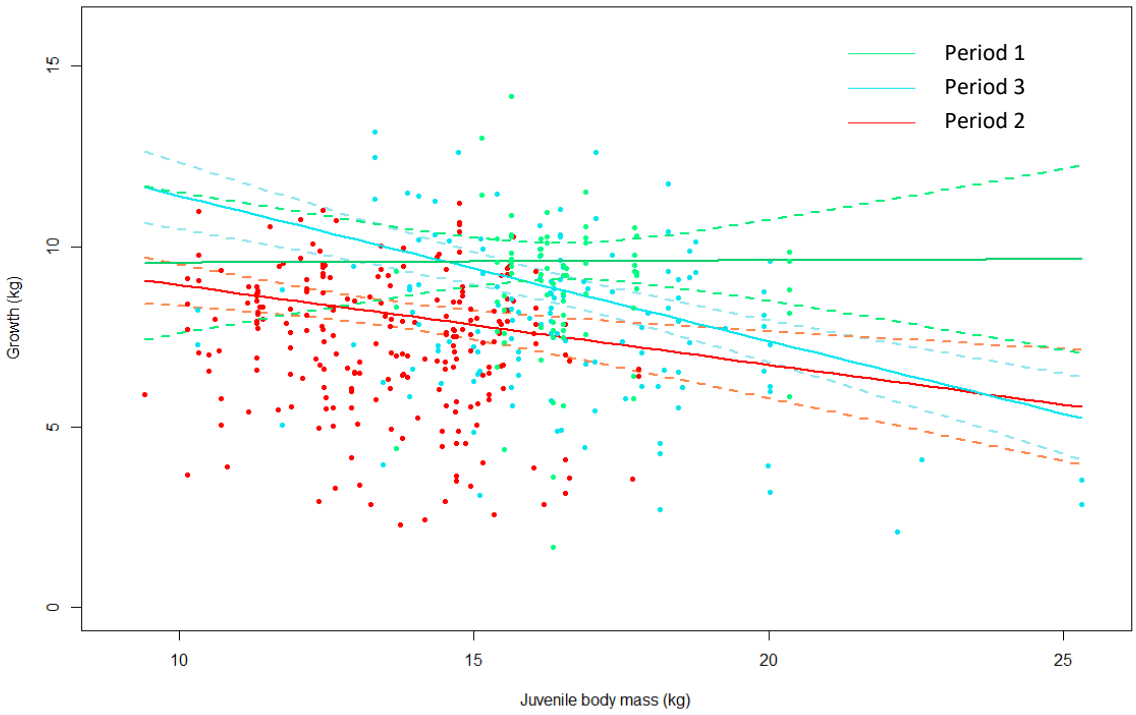


Figure 2: Variations in male growth (kg) as a function of increasing juvenile body mass (kg) for three periods (1: 1982 to 1993, 2: 1994 to 2002 and 3: from 2003 onwards). The lines (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Points represent the observed growth values for a given juvenile body mass.

b. Variations of growth from juvenile to yearling stage

The retained model contained the effect of period (Table S4). Male growth decreased by about 20% from period 2 to period 3 (estimate of -1.55 ± 0.53 kg, N=95 – Table S5, Fig. 3).

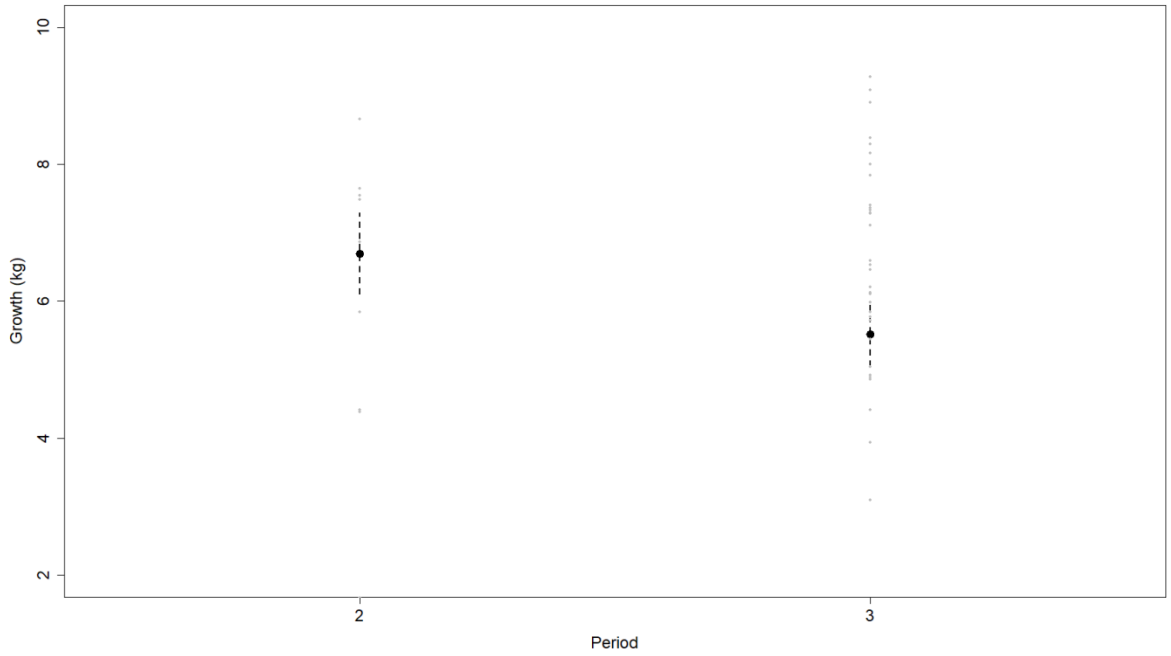


Figure 3: Variations in male growth from the juvenile to the yearling stage for two periods (2: 1994 to 2002 and 3: from 2003 onwards). The black dots (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Grey points represent the observed growth values for the two periods.

c. Adult and senescent growth

When studying male growth from yearling to adult stage, we found that the quality of settlement sector had an influence on growth (Table S6). Individuals settling in the poor quality sector presented a growth from the yearling to the adult stage about 30% higher compared to individuals which settled in the rich quality sector (estimate of 1.01 ± 0.13, N=46, Fig. 4). Because the sample size to study growth from the adult to the senescent stage in males was too small (4 observations on only two individuals), we did not realise this last analysis on males.

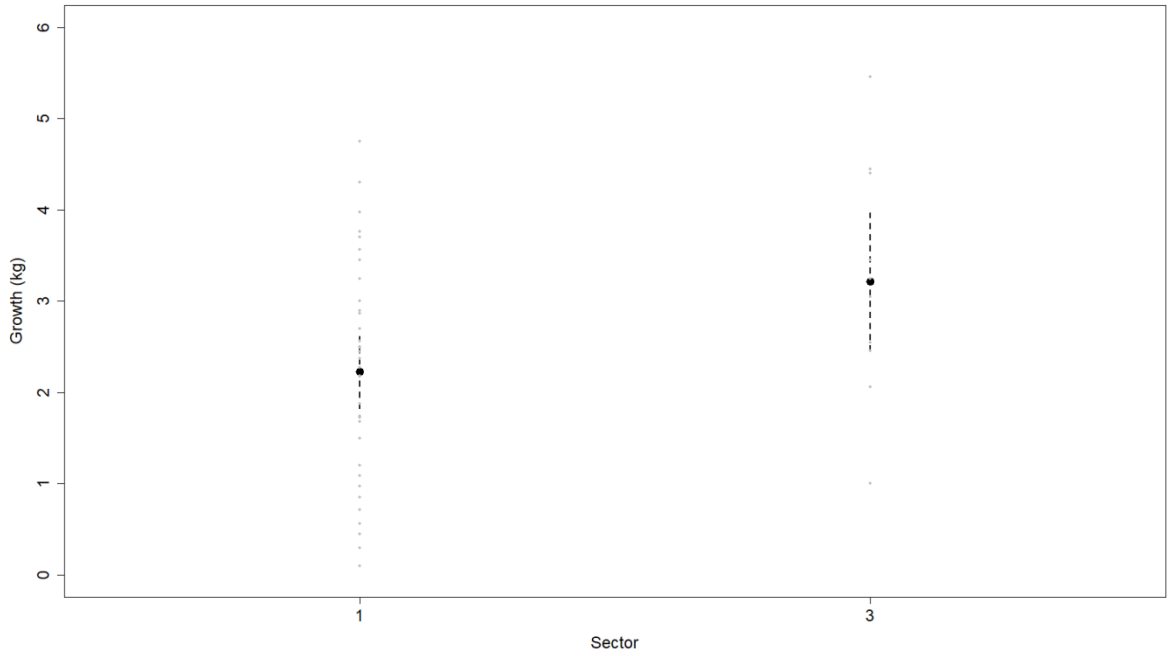


Figure 4: Variations in male growth from the yearling to the adult stage for two sector qualities (good quality: sector 1 and bad quality: sector 3). The black dots (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Grey points represent the observed growth from the yearling to the adult stage for the two sectors.

2) Variations of growth in females

a. Variations of growth throughout the entire life

Analyses showed that female growth varied non-linearly with age, and that this relationship was not affected by dispersal status (Supplementary Materials Annex II 1) and 2)). We thus modelled the age effect on female growth using a non-specific thin-plate regression spline. The retained model describing female growth contained the additive effects of body mass and period (Table S9). Female growth decreased linearly with increasing juvenile body mass (estimate of -0.45 ± 0.67 kg per kg of juvenile body mass – Table 2, Fig. 5), indicating females were gaining less weight if they were heavy as juveniles. Female growth increased approximately until 6 years old, stabilised and then decreased

from 8 years old (Fig. 6, Table 2). We did not detect a significant variation in female growth from period 1 to 2. However, female growth decreased from period 2 to 3 (estimate of -1.32 ± 0.41 kg, N=183) or period 1 to period 3 (estimate of -2.03 ± 0.44 kg) (Table 2 and Fig. 7). Thus, females are getting less and less weight from a given juvenile body mass over periods.

Table 2: Summary statistics of the retained gamm model describing female growth from juvenile stage across an individual's life in relation to body mass and period. We report parameter estimates (±SE) for each variable that featured in the retained models, t values, and p-value, for two different periods chosen as reference values for the model. For smooth effects, we give the effective degrees of freedom (edf), the residual degree of freedom (Ref.df), the Wald Statistic (Chi.sq) and the p-value. Significant effects are indicated in bold writing.

Parameters	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept – Reference = Period 1)	14.97	1.00	15.04	< 0.001
Mass	**-0.45**	**0.07**	**-6.78**	< 0.001
Period 1 to2	-0.71	0.48	-1.48	0.14
Period 1 to 3	**-2.03**	**0.44**	**-4.59**	**< 0.001**
(Intercept – Reference = Period 2)	**14.26**	**1.10**	**12.96**	**< 0.001**
Mass	**-0.45**	**0.07**	**-6.78**	**< 0.001**
Period 2 to 1	0.71	0.48	1.84	0.14
Period 2 to 3	**-1.32**	**0.41**	**-3.21**	**0.001**
Smooth effects :				
	edf	Ref.df	F	p-value
Random effect of cohort	**10.73**	**24.00**	**16.70**	**0.004**
Random effect of Individual identity	**118.82**	**179.00**	**4.41**	< 0.001
s(Age)	**8.88**	**8.99**	**25.50**	< 0.001

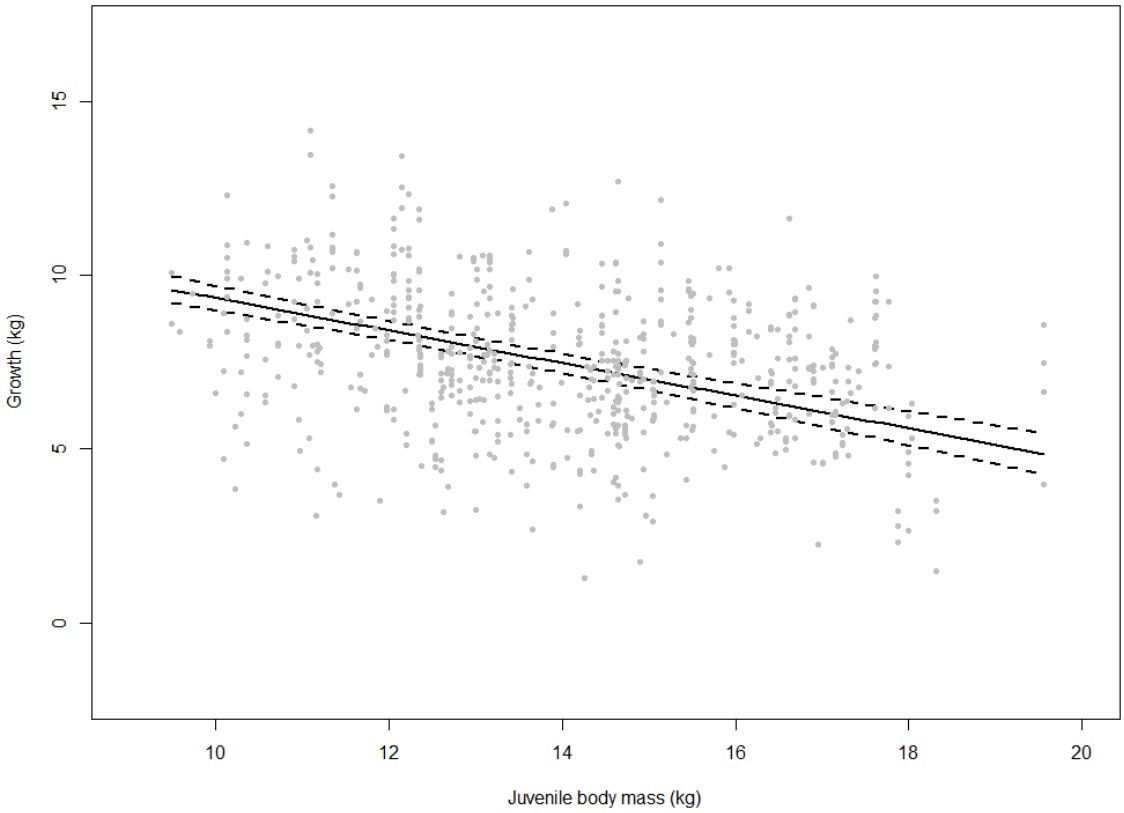


Figure 5: Variations in female growth (kg) with increasing juvenile body mass (kg) across the individual's life. The line (and dotted lines) represents the model predictions (and the associated 95% confidence intervals). Grey points represent the observed growth values for increasing juvenile body mass.

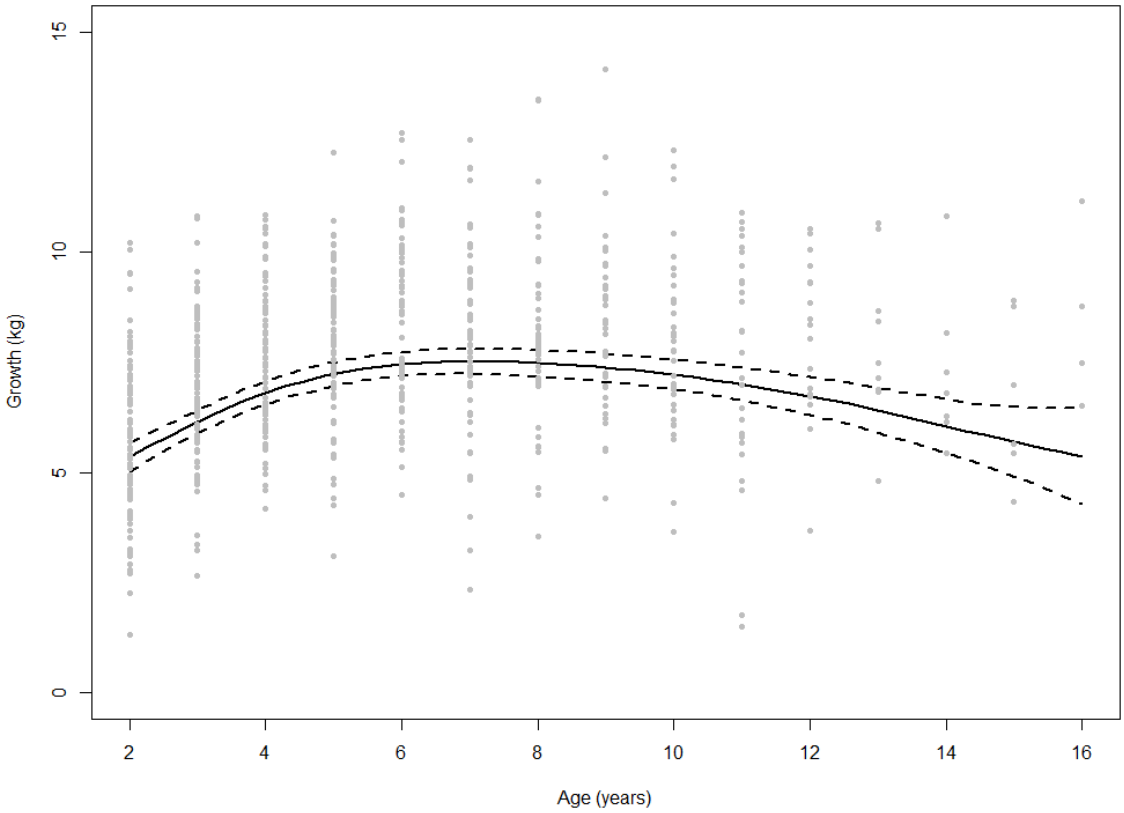


Figure 6: Variations in female growth (kg) from the juvenile stage in relation to age. The line (and dotted lines) represents the model predictions (and the associated 95% confidence intervals). Points represent the observed growth with age. Grey points represent the observed growth values for the increasing age.

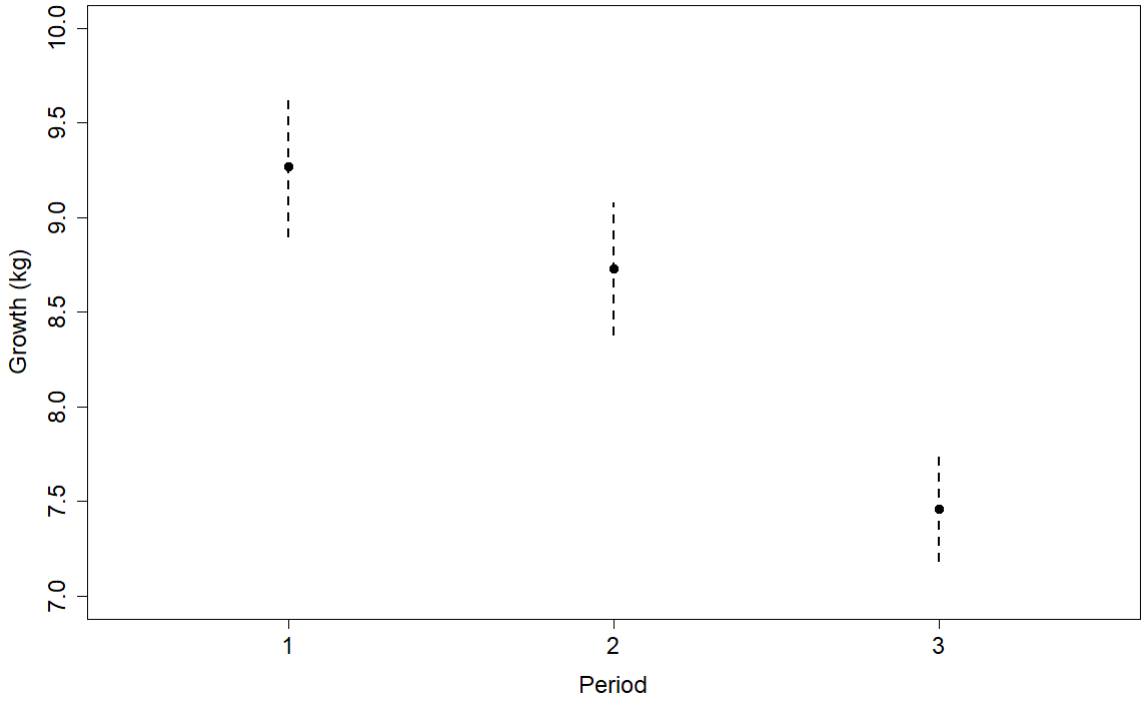


Figure 7: Variations in female growth (kg) from the juvenile stage across an individual's life for three periods. Periods: 1: 1982 to 1993, 2: 1994 to 2002, 3: 2003 to 2015. The black dots (and dotted lines) represent the model predictions (and the associated 95% confidence intervals).

b. Variation of growth from juvenile to yearling stage

The best model describing female growth from juvenile to yearling stage contained the additive effects of body mass and period (Table S10). Female growth decreased linearly with juvenile body mass (estimate of -0.25 ± 0.11 kg per kg of juvenile body mass, N=94 – Table 3 and Fig. 8). We did not detect any variation of growth between periods 1 and 2, however, it decreased by about 17% from period 2 to 3 (estimate of -1.79 ± 0.70 kg, N=94 – Table 3 and Fig. 9), indicating females have been gaining less weight from the juvenile to the yearling stage in the past 15 years.

Table 3: Summary statistics of the retained gamm model describing female growth from juvenile stage to the yearling stage in relation to body mass and period. We report parameter estimates (±SE) for each variable that featured in the retained models, t values, and p-value. Significant effects are indicated in bold writing. For smooth effects, we give the effective degrees of freedom (edf), the residual degree of freedom (Ref.df), the Wald Statistic (Chi.sq) and the p-value. Significant effects are indicated in bold writing.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	10.23	1.75	5.86	< 0.001
Body mass	**-0.25**	**0.11**	**-2.37**	**0.02**
Period 1	0.06	0.86	0.07	0.95
Period 3	**-1.79**	**0.70**	**-2.57**	**0.01**
Smooth effect :				
	edf	Ref.df	F	p-value
Random effect of cohort	**12.52**	**21**	**2.098**	**<0.001**

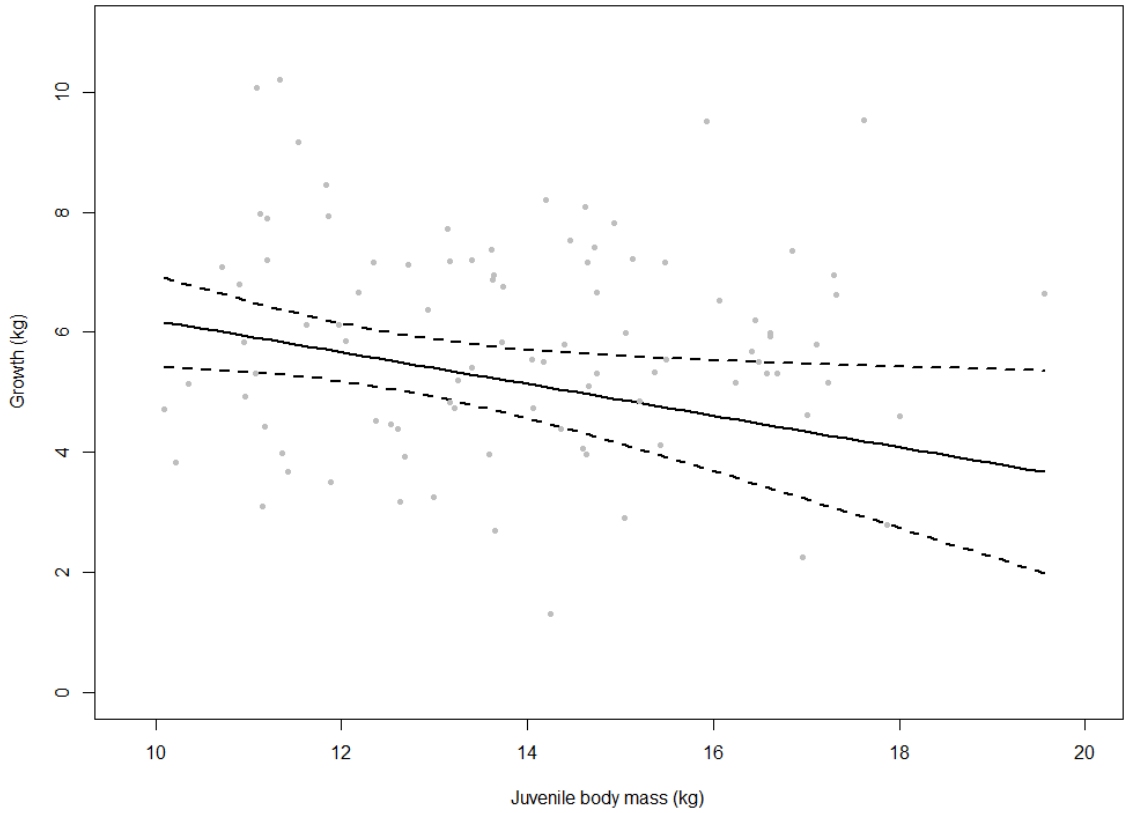


Figure 8: Variations in female growth (kg) from the juvenile stage to the yearling stage as a function of increasing juvenile body mass (kg). The lines (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Grey points represent the observed growth for a given juvenile body mass.

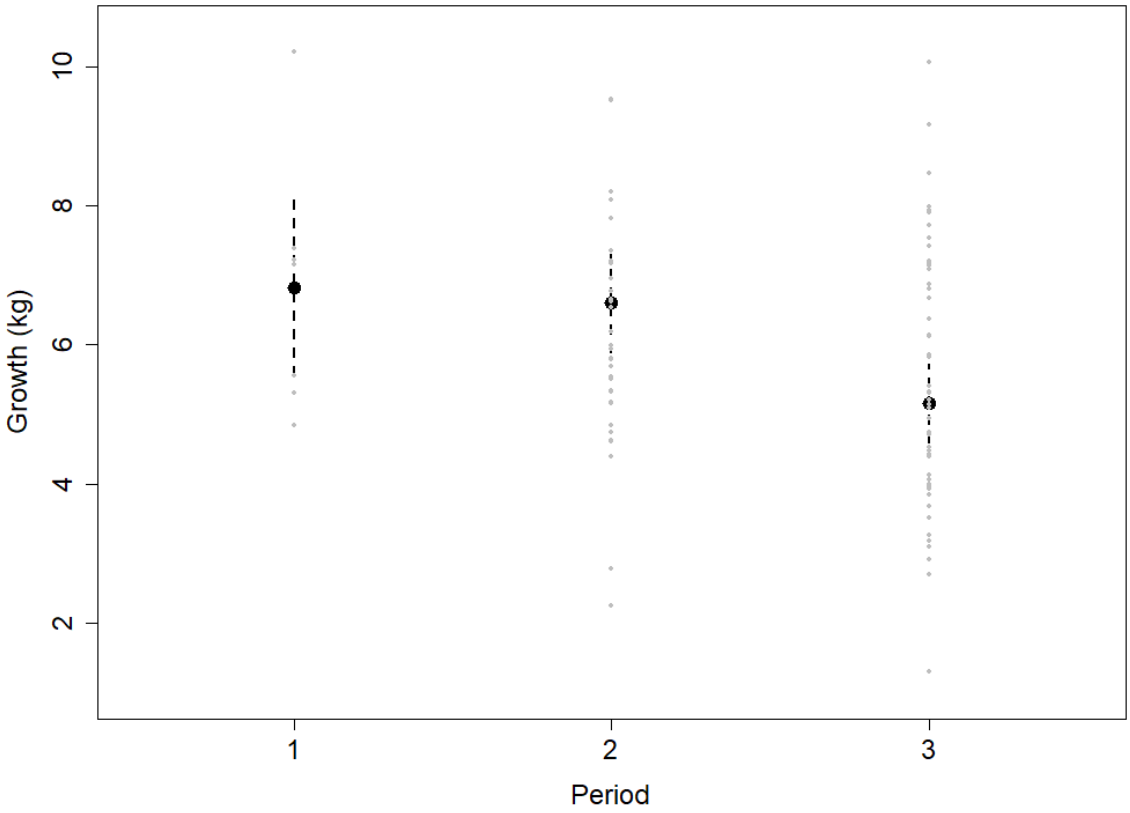


Figure 9: Variations in female growth (kg) from the juvenile stage to the yearling stage for three periods (1: 1982 to 1993, 2: 1994 to 2002, 3: 2003 to 2015). The black dots (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Grey points represent the observed growth values for the three periods.

c. Variation of growth from yearling to adult stage

The best model describing female growth from yearling to adult stage contained the additive effects of period and juvenile body mass (Table S11). Juvenile body mass had a negative impact on female growth (estimate of -0.27 ± 0.11 kg per kg of juvenile body mass, Table 4 and Fig. 10). Female growth decreased from period 1 to period 2 by about 18% (estimate of -1.26 ± 0.59 kg, N=62) but the decrease from period 1 to 3 (estimated to ~ 14%) was only marginally significant (p-value = 0.07) (Table 4 and Fig. 11). Thus, females gained less weight in the period from 1994 to 2002 compared to

prior 1994, but since 2003, this effect has weakened and females are not gaining as little weight as between 1994 and 2002.

Table 4: Summary statistics of the retained gamm model describing female growth from the yearling stage to the adult stage in relation to juvenile body mass and period. We report parameter estimates (±SE) for each variable that featured in the retained models, t values, and p-value. Significant effects are indicated in bold writing. For smooth effects, we give the effective degrees of freedom (edf), the residual degree of freedom (Ref.df), the Wald Statistic (Chi.sq) and the p-value. Significant effects are indicated in bold writing.

Parameter	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	7.18	1.36	5.27	< 0.001
Body mass	**-0.30**	**0.09**	**-3.26**	**0.002**
Period 2	**-1.26**	**0.59**	**-2.14**	**0.04**
Period 3	-1.04	0.55	-1.89	0.07
Smooth effects				
	edf	Ref.df	F	p-value
s(birth_cohort)	**9.72**	**20**	**1.08**	**0.01**

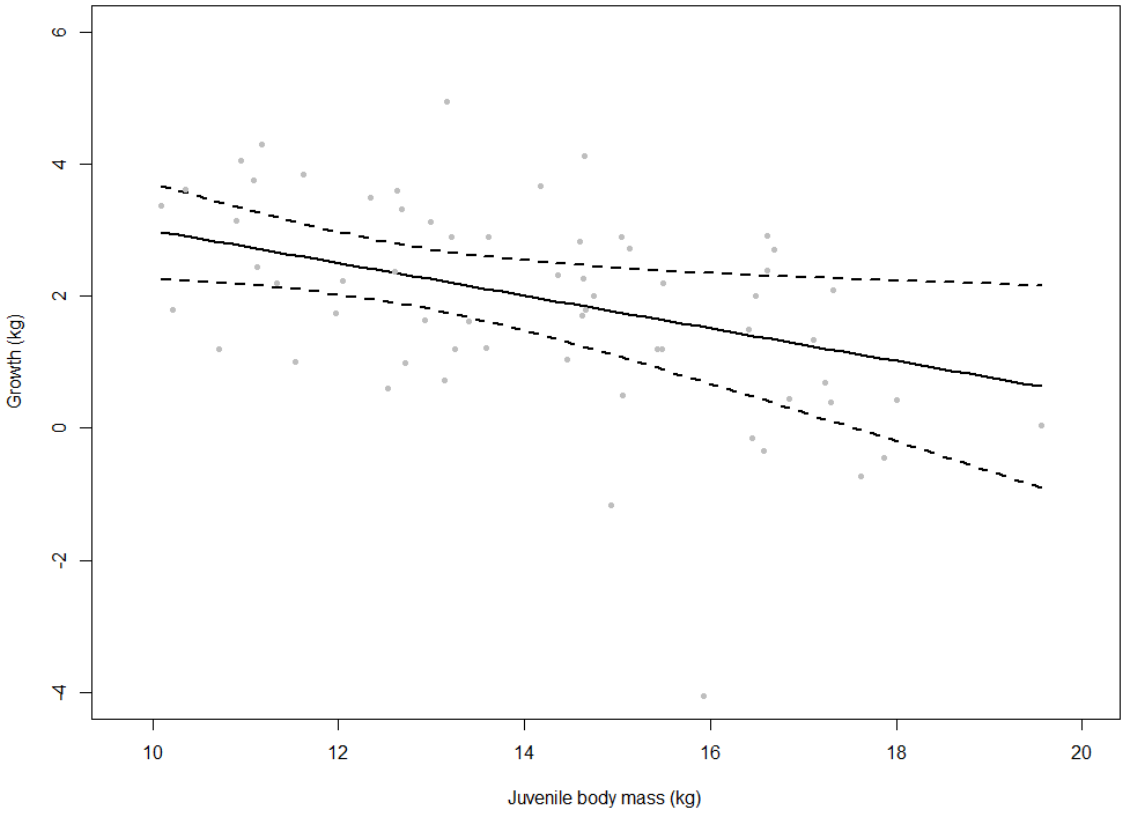


Figure 10: Variations in female growth (kg) from the yearling stage to the adult stage as a function of increasing juvenile body mass (kg). The lines (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Points represent the observed growth for a given juvenile body mass.

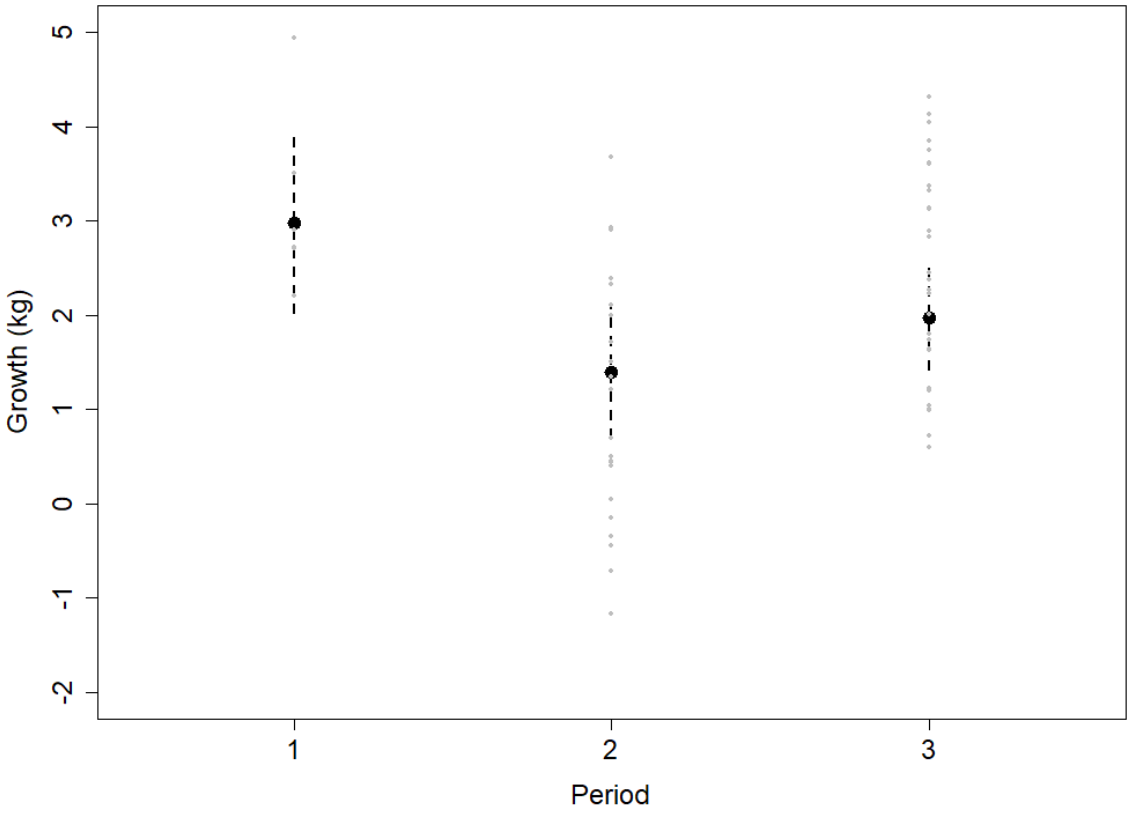


Figure 11: Variations in female growth (kg) from the yearling stage to the adult stage for three periods (1: 1982 to 1993, 2: 1994 to 2002, 3: 2003 to 2015). The black dots (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Grey points represent the observed growth values for the three periods.

d. Variation of growth from adult to senescent stage

Because we lacked statistical power due to reduced sample size (N=13), we ran fewer models for this analysis (see list in Table S12). The retained model contained the additive effects of body mass and dispersal status (Table S12). Dispersal status had a significant effect , however, body mass seemed to have a low statistical support (p-value = 0.24 – Table 5). Dispersers lost about 40% more weight at senescence compared to philopatric individuals in females (estimate of -0.70 ± 0.19 kg, N=13 – Table 5 and Fig. 12).

Table 5: Summary statistics of the retained gamm model describing female growth from adult to senescent stage in relation to body mass and dispersal status. We report parameter estimates (±SE) for each variable that featured in the retained models, t values, and p-value. Significant effects are indicated in bold writing.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	0.02	0.64	0.03	0.98
Body mass	-0.06	0.04	-1.35	0.24
Status Disperser	**-0.70**	**0.19**	**-3.70**	**0.01**
Smooth effect :				
	edf	Ref.df	F	p-value
Random effect of cohort	5.16	9.00	1.94	0.10

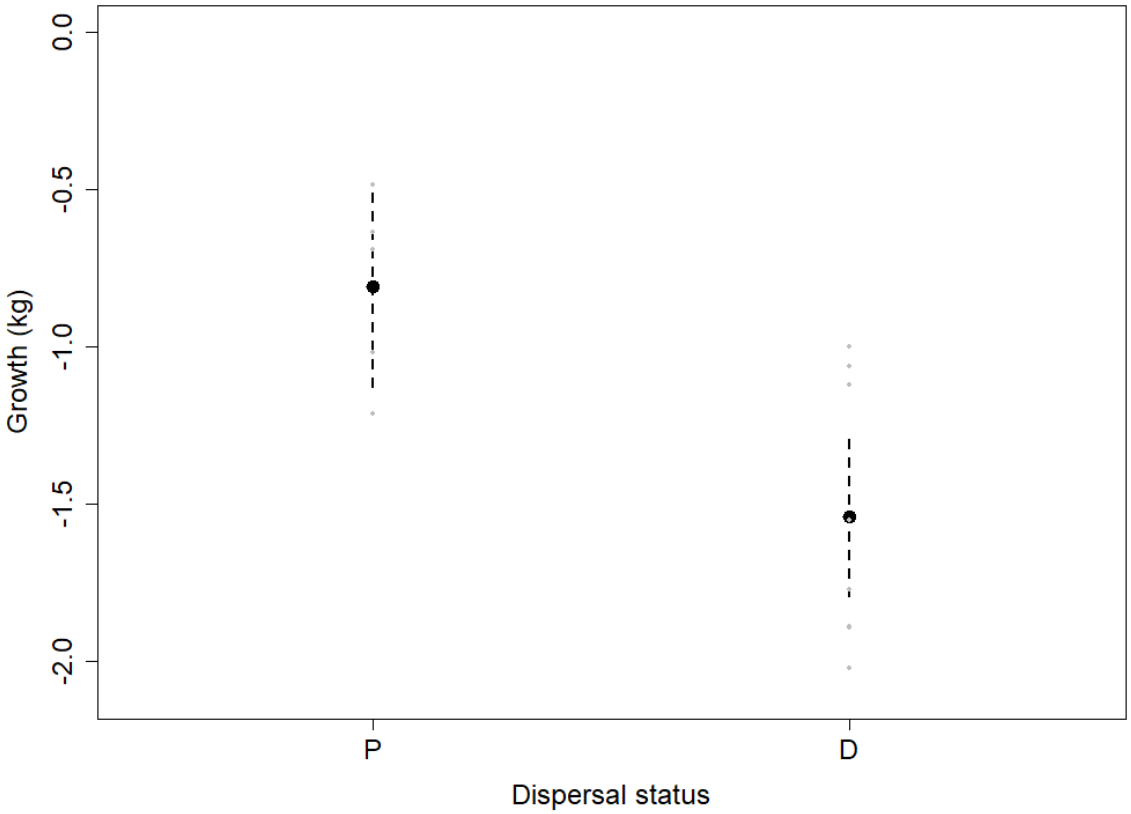


Figure 12: Variations in female growth (kg) from the adult stage to the senescent stage for two dispersal statuses (D: Disperser; P: Philopatric individual). The black dots (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Grey points represent the observed growth values for the two dispersal statuses.

II- Reproductive success analyses

1) Probability to reproduce

The best model of the effect of age on P_{rep_tot} contained a threshold effect at 10 years old, indicating P_{rep_tot} started to decrease from 10 years old onwards (Supplementary Materials Annex III Table S13, Fig. 13). When including the effect of dispersal status and body mass at the year of reproduction measures, the set of retained models contained the effects of body mass and the threshold effect of age at 10 years old (Tables S14 and S15). We also noted a tendency of P_{rep_tot} to vary with the

dispersal status: philopatric individuals had an overall higher probability to reproduce compared to dispersers (by ~ 3%), although the effect size was rather small (Table S15). We thus based our subsequent models on an effect of age specific for each dispersal status.

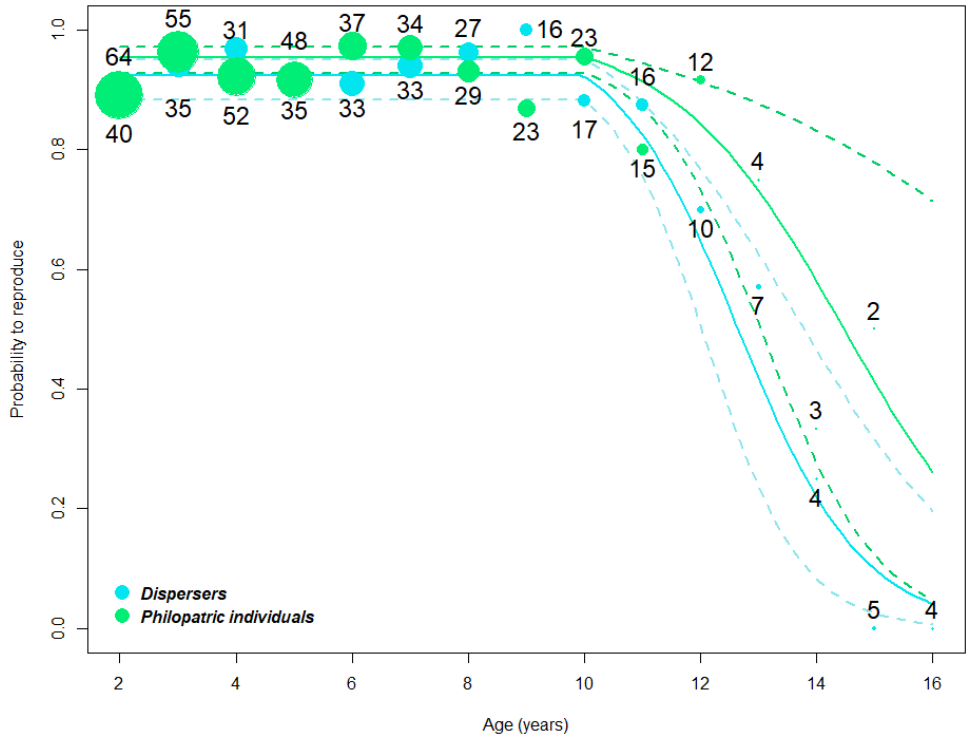


Figure 13: Variations in female propensity to reproduce throughout its life in relation to age and dispersal status. The line (and dotted lines) represents the model predictions (and the associated 95% confidence intervals). Points (centred for intervals of 1 year) represent the observed propensity to reproduce at a given age for a given dispersal status.

a. Probability to reproduce throughout life

The best model describing P_{rep_tot} contained the interactive effect of dispersal status and body mass, as well as the effect of age (Table S16). The probability to reproduce increased with body mass until approximately 22 kg in philopatric individuals, where it reached a value of 1, and remained to this value (Fig. 14, Table 6 – N = 203). In dispersers, the probability was rather constant and high (~0.9)

whatever the body mass (Fig. 14, Table 6 – N = 203), and became lower compared to philopatric individuals around 22kg.

Table 6: Summary statistics of the retained glmer model describing female propensity to reproduce throughout its life in relation to body mass, age and dispersal status. We report parameter estimates (±SE) for each variable that featured in the retained models, t values, and p-value. For random effects, we report the variance and standard deviation for each effect. Significant effects are indicated in bold writing.

	Estimate	Std. Error	t value	Pr(>|t|)
Intercept	0.39	2.46	0.16	0.88
Age	**-0.98**	**0.18**	**-5.53**	**<0.001**
Status Philo	**-6.33**	**3.09**	**-2.05**	**0.04**
Body mass	0.11	0.11	0.98	0.33
Age:status P	0.19	0.27	0.68	0.50
Status Philo * Body mass	**0.33**	**0.15**	**2.29**	**0.02**
Random effects :				
Parameter	edf	Ref.df	Chi.sq	p-value
Cohort	6.15	27	9.29	0.19
Random effect of individual identity	24.49	201	33.26	0.01

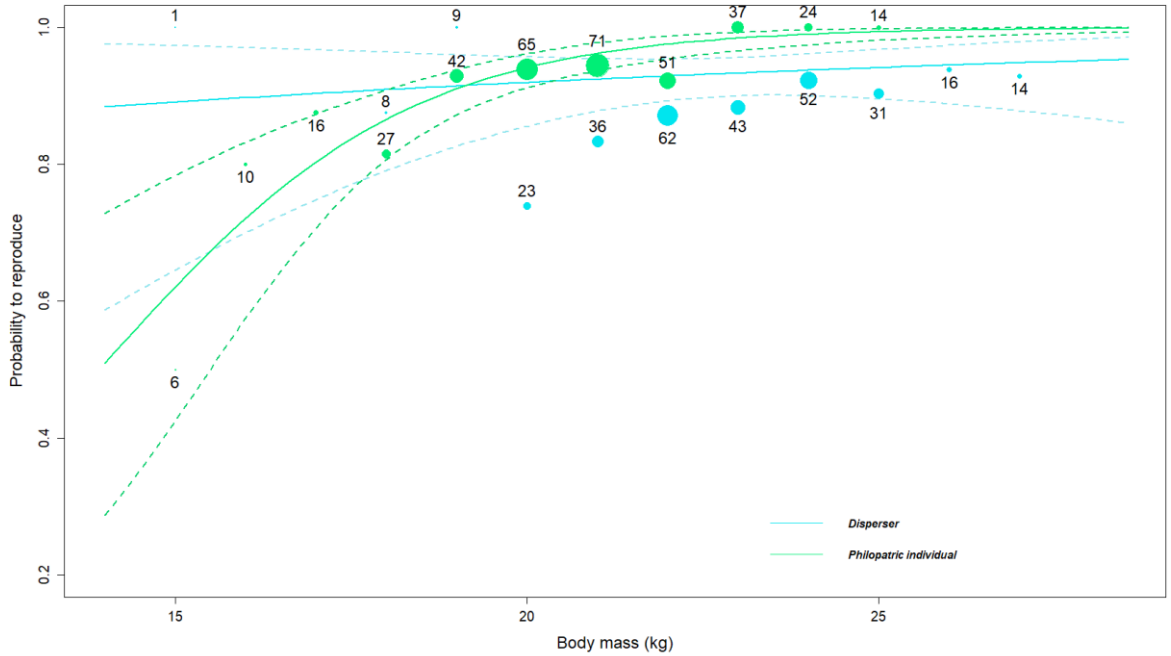


Figure 14: Variations in the propensity to reproduce throughout an individual's life as a function of increasing body mass (kg) for two dispersal statuses (in blue: dispersers and in green: philopatric individuals). The lines (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Points (proportional to sample size and centred for intervals of 1 unit of body mass) represent the observed propensity to reproduce for a given body mass.

b. Probability to reproduce at two years old

The best model describing the propensity to reproduce at two years old contained the linear effect of body mass (Table S17). P_{rep2} increased non-linearly with body mass (estimate of 0.31 ± 0.13, N=104 – Figure 15). Heavier individuals had a higher probability to reproduce at two years old, with a probability to reproduce around 0.6 for light individuals of 15 kg while it reached 1 for heavy individuals of 25 kg.

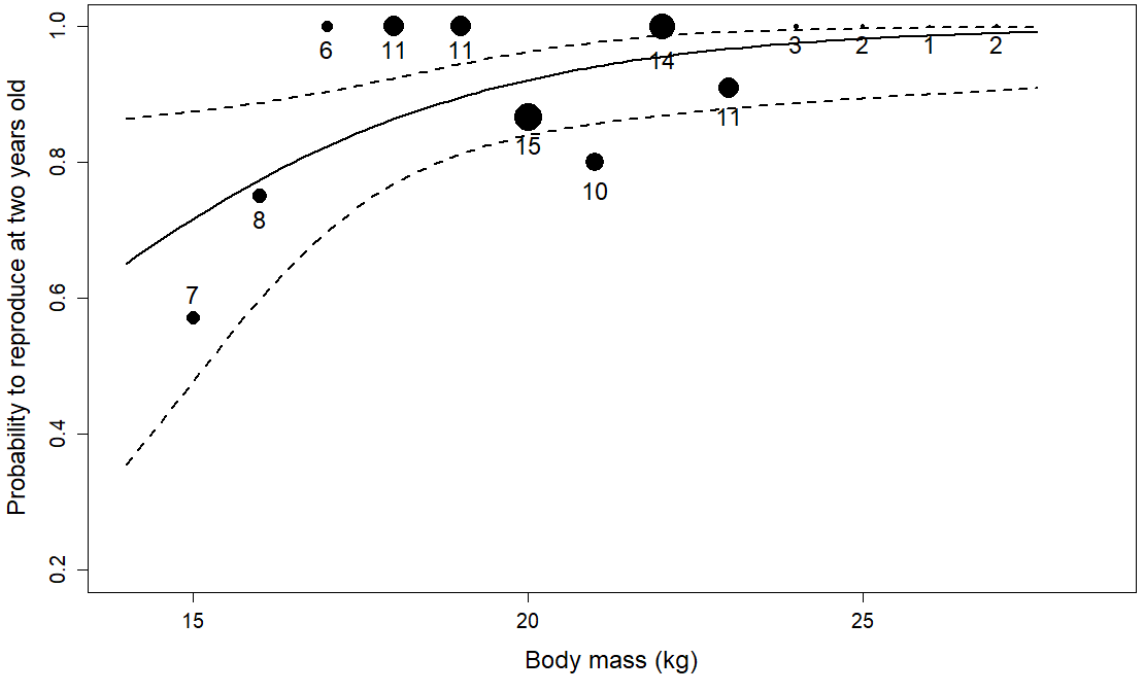


Figure 15: Variations in the propensity to reproduce at two years old as a function of increasing body mass (kg). The lines (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Points (proportional to sample size and centred for intervals of 1 unit of body mass) represent the observed propensity to reproduce for a given yearling body mass.

2) Probability to get more than one embryo

a. Probability to get more than one embryo throughout life

The best model of the effect of age contained a smoothed effect of age differing for each dispersal status (see Supplementary Materials Annex III Tables S18, S19). The effect of age was hence modelled using a thin plate regression spline specific for each dispersal status, using gamm models.

The best model describing the propensity to get more than two embryos contained the effect of body mass, in addition to the smoothed effect of age specific for each dispersal status (Table S20). P_{emb_tot} increased with increasing body mass (estimate of 0.52 ± 0.06, N= 193, Fig. 16, Table 7), indicating individuals had approximately four times higher probability to get more than one embryo if they were equal or above 22 kg compared to lighter individuals of 16~18kg. In dispersing

individuals, P_{emb_tot} started with mean values above those of philopatric individuals, and decreased almost linearly with age (Fig. 17). On the contrary, in philopatric individuals, P_{emb_tot} increased up until 6 years of age, and then decreased, but results suggest that the probability to get more than one embryo still remains higher in the senescent phase for philopatric individuals, although we have a very small sample size for these old ages.

Table 7: Summary statistics of the retained gamm model describing female propensity to have more than one embryo throughout its life in relation to period (when body mass was included in the model selection). We report parameter estimates (±SE) for each variable that featured in the retained models, t values, and p-value. For smooth effects, we give the effective degrees of freedom (edf), the residual degree of freedom (Ref.df), the Wald Statistic (Chi.sq) and the p-value. Significant effects are indicated in bold writing.

Parameters	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-10.50	1.33	-7.87	< 0.001
masse	**0.52**	**0.06**	**8.46**	**< 0.001**
Smooth effects :				
Parameter	edf	Ref.df	Chi.sq	p-value
Random effect of cohort	9.12	27.00	16.11	0.13
Random effect of individual identity	28.17	192.00	35.09	0.07
s(age):status Disperser	**1.00**	**1.00**	**6.37**	**0.01**
s(age):status Philopatric	2.76	3.45	4.49	0.27

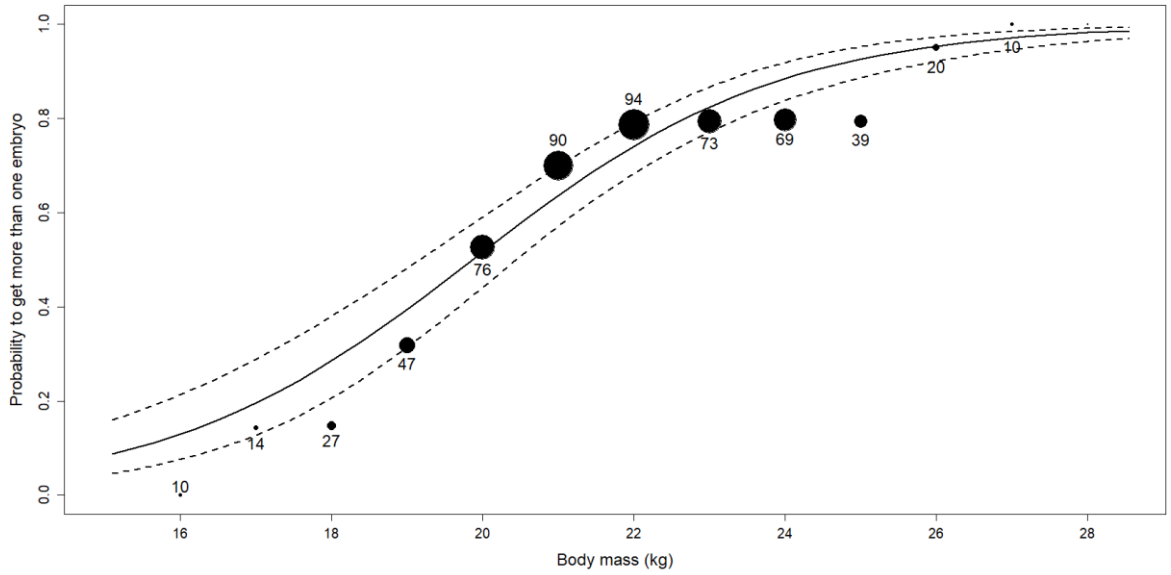


Figure 16: Variations in the propensity to get more than one embryo when reproducing throughout an individual's life as a function of increasing body mass (kg). The lines (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Points (proportional to sample size and centred for intervals of 1 unit of body mass) represent the observed propensity to get more than one embryo for a given body mass.

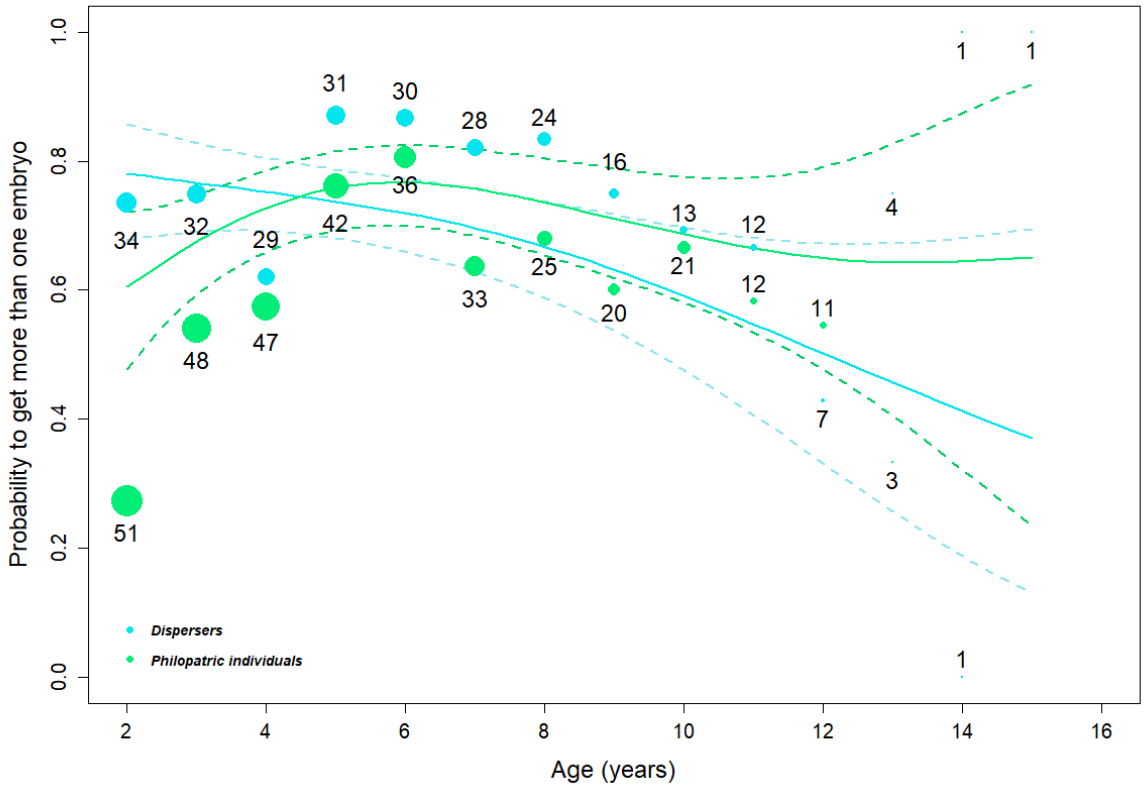


Figure 17: Variations in the propensity to get more than one embryo when reproducing throughout an individual's life as a function of increasing age for two dispersal statuses (in blue: dispersers and in green: philopatric individuals). The lines (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Points (proportional to sample size and centred for intervals of 1 year of age) represent the observed propensity to get more than one embryo for a given age.

b. At two years old

The set of retained models describing the propensity to get more than one embryo at two years old (P_{emb2}) contained the effect of body mass (Table S21). P_{emb2} increased non-linearly with body mass (estimate of 1.06 ± 0.23, N= 79), with light individuals (body mass inferior to 20 kg) having a P_{emb2} value between 0 and 0.2 and heavy individuals (body mass superior to 22 kg) having a P_{emb2} value above 0.8 (Fig. 18).

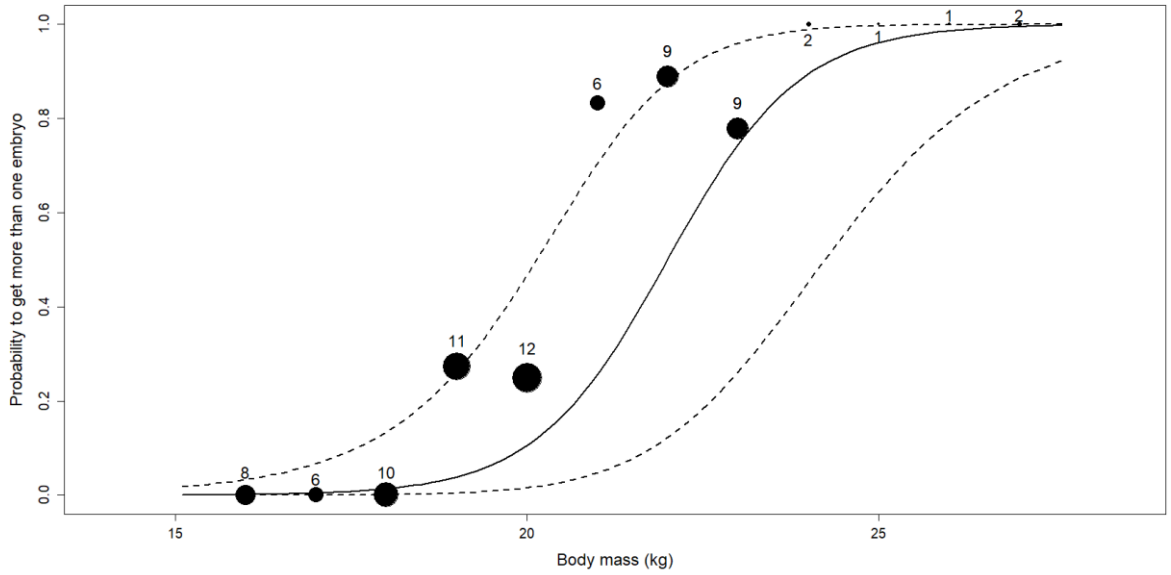
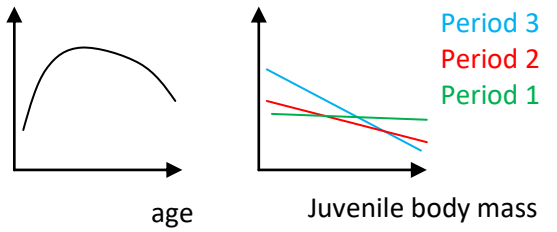
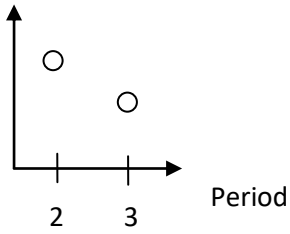
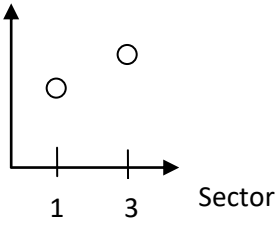
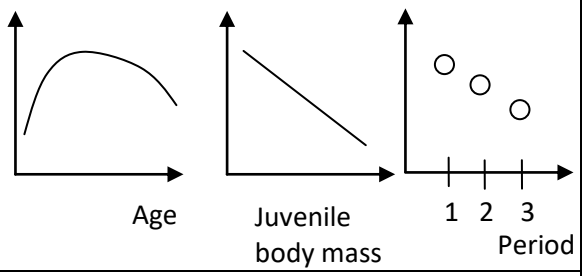
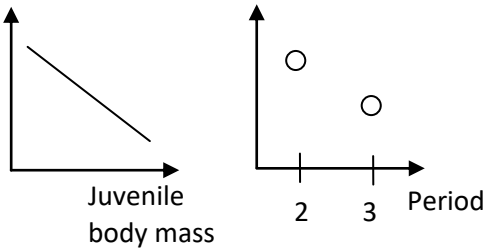
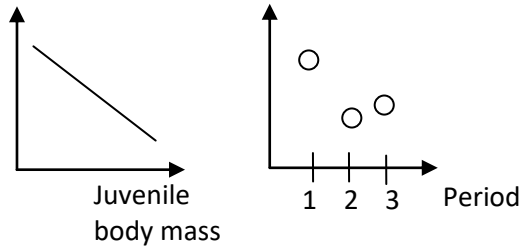
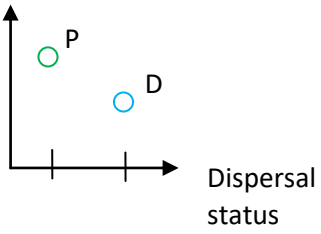
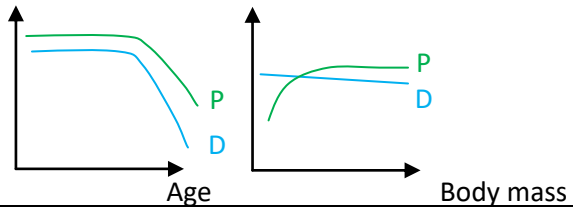
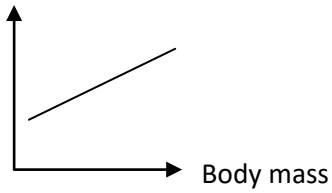
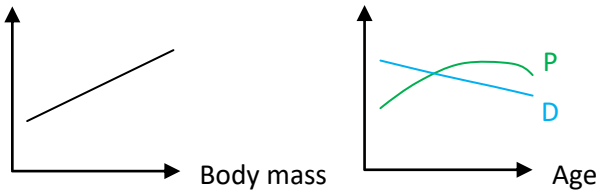
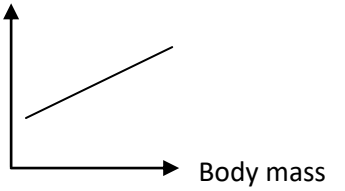


Figure 18: Variations in the propensity to get more than one embryo at two years old as a function of increasing body mass (kg). The lines (and dotted lines) represent the model predictions (and the associated 95% confidence intervals). Points (proportional to sample size and centred for intervals of 1 unit of body mass) represent the observed propensity to get more than one embryo.

Table 8: Table summarizing all results obtained both in the analyses on growth (1) and reproduction (2)

<table>
<tr><th colspan="4">1) BODY GROWTH</th></tr>
<tr><td rowspan="5">Body growth</td><td rowspan="3">Males</td><td>Entire life</td><td> 
</td></tr>
<tr><td>Two years old</td><td> 
</td></tr>
<tr><td>Adult</td><td> 
</td></tr>
<tr><td>Senescent</td><td>Not assessed</td></tr>
<tr><td rowspan="2">Females</td><td>Entire life</td><td> 
</td></tr>
<tr><td>Two years old</td><td> 
</td></tr>
</table>

<table>
<tr><td rowspan="2"></td><td rowspan="2"></td><td>Adult</td><td> 
</td></tr>
<tr><td>Senescent</td><td> 
</td></tr>
<tr><td colspan="4"></td></tr>
<tr><td colspan="4">(2) REPRODUCTION</td></tr>
<tr><td rowspan="2">Probability to reproduce (P_{rep})</td><td>During entire life</td><td colspan="2"> 
</td></tr>
<tr><td>At two years old</td><td colspan="2"> 
</td></tr>
<tr><td rowspan="2">Probability to have more than one embryo (P_{emb})</td><td>During entire life</td><td colspan="2"> 
</td></tr>
<tr><td>At two years old</td><td colspan="2"> 
</td></tr>
</table>

Discussion

In this study, we wished to assess whether or not dispersal may lead to medium or late life costs to individuals, both in terms of reproduction and growth, and if this effect may be influenced by climate change. We did not show any interaction between dispersal costs and climate change per se. However, we did find both of these factors to have an effect on growth, and only an effect of dispersal status on reproduction. In males, we found that growth was lower when environmental conditions deteriorated, especially for light juveniles. However, dispersal did not appear to lead to any cost. Surprisingly, we also found that growth from the juvenile to the adult stage was higher for individuals living in poor-quality habitats in males. In females, we found both effects of periods and dispersal on reproduction and growth: female dispersers presented a stronger body mass senescence and seemed to have a reduced reproductive success both in terms of reproductive events and number of embryos produced during senescence stage. Moreover, female growth decreased when environmental conditions deteriorated, indicating climate change may have consequences on individual condition, with potential cascading effects on other life-history traits.

Trade-offs are directly linked to individuals' life histories, by imposing boundaries to individual's capacities in each trait for a particular environment (Stearns 1989, Agrawal et al. 2010). Our results suggest the existence of a trade-off between the dispersal process occurring in early life and body mass and reproduction in late-life, but only in females. Because females outlive males in this species (Gaillard et al. 2004, see Chapter 1 for survival estimates for this dataset), we had more senescent females and were able to detect this direct effect of dispersal status on body mass during the senescence phase, while we may not have been able to detect it in males because of low sample size. Consistent with the pace-of-life hypothesis (Réale et al. 2010), we showed that (i) the probability to reproduce tended to senesce more rapidly in dispersing individuals (about twice faster), (ii) female dispersers had a higher probability to get more embryos at early ages compared to philopatric individuals, (iii) females tended to have a lower reproductive success (i.e. number of embryos) at old

ages compared to philopatric females, and (iv) at the senescent stage, dispersing females lost more weight compared to philopatric females. Hence, high investment in early life in terms of dispersal and reproduction may lead to the observed increased senescence in reproductive probability in females, consistent with recent but still scarce works demonstrating long-term senescence costs of dispersal (Bouwhuis et al. 2010, Nevoux et al. 2013, Dingemanse et al. 2019). For example, Bouwhuis et al. 2010 found that dispersing individuals suffered from faster rates of senescence than resident individuals, leading to a lowered lifetime reproductive success for these individuals. Nevoux et al (2013) showed similar results in terms of reproduction and demonstrated that lifetime reproductive success also decreased with increasing distance. This result may be explained for two main reasons. First, the high reproductive performance of females in early life suggests that dispersal may be highly beneficial for dispersing females, despite potential dispersal costs, as it could allow them to reach favourable habitats compared to philopatric individuals (potentially at the parcel level, and not at the sector level, as the latter was not detected in the models). These habitats could allow dispersers to benefit from high-quality resources or mates, and thus, have a high growth and reproductive success at the beginning of their life. Second, in a mechanistic way, the long-term effects of dispersal may be mediated by the energetic costs of dispersal (Bonte al. 2012). Because dispersers are allocating a lot of energy to disperse and to other related-traits, such as growth (Debeffe et al. 2012, Benoît et al. 2019), they are increasing the amount of cellular damage in their body and allocating fewer amount of energy to somatic maintenance which both lead to increased senescence (Kirkwood and Rose 1991, Careau et al. 2008). The decrease in reproductive performance could be directly linked to the somatic deterioration, which, in our case, could result from both an early and intense use of energy from young roe deer to reproduce and disperse (Lemaître et al. 2015).

In recent years, growing research has been suspecting that climate change may be increasing dispersal costs (Massot et al. 2008, Bonte et al. 2012). In this work, we did not find any support for this hypothesis. Several explanations could account for this effect. First, this effect could suggest that the modifications of the environment due to climate change may not be critical for dispersal per se,

for example because they might not impact resources that roe deer use for dispersal, or that because of the highly plastic behaviour of roe deer, the latter may change its nutritive behaviour in function of the available resources (Abbas et al. 2011, Serrano Ferron et al. 2012). Alternatively, the high quality of roe deer dispersers (Debeffe et al. 2012) could allow them to perform well despite bad environmental conditions, as has been shown in other species (for example in Monteiro's storm petrel (*Oceanodroma monteiroi*), Robert et al. 2012). However, climate change still had effects on growth, which strongly decreased in both sexes as environmental conditions deteriorated. This effect was not expressed in the same way in both sexes. Indeed, in males, growth between the juvenile stage and other ages depended on the interaction between period and body mass, with a higher slope in the third period compared to the second, indicating that individuals are gaining less and less weight from their juvenile body mass as climate changes, especially light individuals. This result suggests that when environmental conditions deteriorate, light individuals may not be able to compensate growth as much as in good environmental conditions, and thus suffer double penalty from climate change (Wilson and Osbourn 1960). Indeed, lighter individuals are in poorer condition compared to heavier individuals, which may already reduce their survival probability at the juvenile stage (Da Silva et al. 2008, Monestier et al. 2015), but if they cannot compensate for their reduced juvenile growth, they may even more be impacted on the long term. We also show that growth throughout the entire life (i.e. between the juvenile stage and other ages) was higher in period 3 than period 2; since environmental conditions are poor in period 3, we expect that juveniles that may have a lower weight compared to if they were in good environmental conditions (Pettorelli et al. 2001), and thus, individuals may have to gain more weight after the juvenile stage to reach adult body mass in these conditions compared to a case where rich habitats provide resources for fawns. Females on the other hand seemed equally affected by climate change, irrespective of their juvenile body mass, confirming that the effects of environmental conditions on body mass and growth are sex-specific in roe deer (Toïgo et al. 2006). We expect that the high energy expenditure that female roe deer spend in early life for reproduction may account for this difference between sexes, as even

heavier females may incur a strong reproductive cost. Because, body mass is strongly related to performance in roe deer (Gaillard et al. 2000, Hewison et al. 2009), juveniles may not be able to reach the necessary body size to maximize their fitness during adulthood. In particular, we may expect cascading effects of a lower growth on other life-history traits, including reproduction. Indeed, our results show that reproductive success increases when body mass is higher, consistently with previous studies in roe deer (Wauters et al. 1995, Vanpé et al. 2010), and thus, a reduction in body mass because of climate change may decreases the overall population reproductive success, with consequences on population dynamics (Gaillard et al. 2000).

Increasingly limited resources should lead to different energy allocation strategies (Messina and Slade 1999, Donaldson et al. 2005), and in particular, may lead to the apparition of emergency life history stages (Wingfield et al. 1998). This short term answer to environmental change, including habitat deterioration, may allow individuals to rather invest in their survival to the detriment of reproduction and growth. This may participate to explain why dispersal propensity decreased in recent years (See Chapter I): because a good body condition is an important prerequisite for successful dispersal (Barbraud et al. 2003, Debeffe et al. 2012, Searcy et al. 2018), the observed decrease in growth with climate change in both sexes might explain the declines in dispersal propensity. Emergency life history has usually been considered a stage in the life cycle of individuals, which thus ends when the perturbation factor ends (Wingfield et al. 1998). However, it may become an issue both at the individual and population levels if this stage is prolonged for a long period of time because climatic conditions continue to deteriorate (Ripple et al. 2019). Indeed, at the individual level, individuals may be of poorer condition and thus, incur lower fitness on the long term (both in terms of survival and reproduction). At the population level, this decrease in fitness should lead to a decrease in population growth rate, and thus, impact population dynamics (Caswell 1978, Gaillard et al. 2000).

Previous work showed that roe deer demographic parameters are not highly sensible to variation in the environment, including variations in resources (Gaillard et al. 2000). This canalization of adult demographic parameters seems rather verified in this study population, as settlement habitat quality was not present in the retained models, except for the analysis on male growth from the yearling to adult phase. Quite surprisingly, male growth from the yearling to adult stage was higher for individuals living in the poor quality sector compared to individuals living in the high quality sector, leading to even higher adult body mass values compared to adults settled in the high quality sector. This result is also contradictory with previous results obtained from this population (Pettorelli et al. 2001, 2002). We suggest that this result may come from the high selection pressures that operate in habitats of poorer quality. Thus, selection may be higher in the poor-quality sector, leading to more mortality at the most vulnerable stage of life, i.e. juvenile stage (Gaillard et al. 2000). As a consequence, the individuals used for the analysis of growth between the yearling and adult stage are individuals which survived throughout the juvenile period in a habitat of poor-quality, i.e. under strong selection pressures, and they may hence be of high quality. On the contrary, selection pressures may be lower in the high quality habitat, and thus, more individuals of poorer quality may survive. This contrast in individual quality could lead to the apparent superior performance in terms of growth demonstrated for individuals living in the poor-quality habitat.

Nilsen et al. (2009) showed that various life-history strategies existed across five European roe deer populations living in contrasted environments, each allowing the population to adapt to its specific environment. Here, we go further by showing the existence of two life-history tactics within a single population, characterised by among-individual differences in dispersal tactics and investments in growth and reproduction. These contrasted life history strategies have been linked to different consequences in terms of fitness depending on environmental conditions (Dingemanse et al. 2004, Réale et al. 2009, Schmid et al. 2019). The two life-history tactics that we identified (i.e. dispersing and investing early in life or preferring philopatry and investing in late life) could therefore provide the population with a good adaptive potential, as expected by the high level of plasticity

demonstrated by roe deer (Andersen et al. 1998). Depending on environmental conditions, the existence of these two tactics may allow adapting better to environmental fluctuations through time and space (Nilsen et al. 2009), if these fluctuations are within the range of environments to which individuals can respond. However, climate change might impose strong pressures to which all tactics may not be well-adapted, and thus, to which individuals may not be able to respond.

Previous work has shown that climate change has led to changes in dispersal strategies, including strong decreases in dispersal propensity (Massot et al. 2008, Bonte et al. 2008, Delattre et al. 2013). Important declines in dispersal propensity have also been shown in the last decades in our study population (see Chapter I). Moreover, depending on the importance of the senescent stage on population growth rate (Caswell 1978, de Kroon et al. 1986), stronger actuarial (see Chapter I) and breeding senescence incurred by dispersers may lead to a decreased population growth rate, which may in turn lead to dispersal counter-selection on larger evolutionary scales. Overall, our results show that dispersers may lose their "reputation" of high-quality individuals in the context of climate change, in particular at older ages. A next step would be to determine the reproductive costs of dispersal for males in a context of climate change, for example using a pedigree. While climate change may induce costs, it has also been shown to provide benefits to dispersers within a population (for example in the side-blotched lizards (Zani 2008)). Thus, more investigations on this population should give an even clearer picture about which variations in life history traits we may expect with current climate change, and if the detrimental effects of climate change we demonstrated may be balanced with benefits. In particular, the combined effects of dispersal and climate change should add to the joint effect of climate change and dispersal on survival that we demonstrated in this population (See Chapter I). Because growth (and potentially in turn reproduction), and survival patterns may all be modified in the current context of climate change, we may expect changes in population dynamics patterns and life history strategies (Bowler and Benton 2005, Burgess et al. 2012). Hence, the next step for this study could be to model the effects of these changes in demographic parameters on population dynamics, notably in terms of population growth

rate, by including the results obtained in this PhD and those from previous work in this population (Gaillard et al. 2013, Plard et al. 2014). Integrating these results into a population dynamics model may provide insights into the potential future demography of that population and the conservation issues that may arise with climate change.

References

Abbas, F. et al. 2011. Landscape fragmentation generates spatial variation of diet composition and quality in a generalist herbivore. – *Oecologia* 167: 401-411.

Agrawal, A. A. et al. 2010. Tradeoffs and negative correlations in evolutionary ecology. – In: Bell, M. A. et al. (eds), *Evolution since Darwin: the first 150 years 150*. – Oxford Univ. Press, pp. 243–268.

Andersen, R. et al. 1998. The European roe deer: the biology of success. – Scandinavian University Press.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. – *The Journal of Wildlife Management* 74: 1175–1178.

Barbraud, C. et al. 2003. Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. – *Journal of Animal Ecology* 72: 246–257.

Barton, K. 2019. MuMIn: Multi-Model Inference. R package version 1.43.6. https://CRAN.R-project.org/package=MuMIn

Bates, D. et al. 2015. Fitting Linear Mixed-Effects Models Using lme4. – Journal of Statistical Software 67: 1–48. doi:10.18637/jss.v067.i01.

Beckman, N. G. et al. 2018. High dispersal ability is related to fast life-history strategies. – *Journal of Ecology* 106: 1349–1362.

Benoit, L., et al. 2019. Accelerating across the landscape: The energetic costs of natal dispersal in a large herbivore. – *Journal of Animal Ecology*.

Blomquist, G. E. 2009. Trade-off between age of first reproduction and survival in a female primate. – *Biology letters* 5: 339–342.

Bonte, D. et al. 2008. Thermal conditions during juvenile development affect adult dispersal in a spider. – *Proceedings of the National Academy of Sciences* 105: 17000–17005.

Bonte, D. et al. 2012. Costs of dispersal. – *Biological Reviews* 87: 290–312.

Bouwhuis, S. et al. 2010. Individual variation in rates of senescence: natal origin effects and disposable soma in a wild bird population. – *Journal of Animal Ecology* 79: 1251–1261.
Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – *Biological Reviews* 80: 205–225.

Burgess, S. C. et al. 2012. How do dispersal costs and habitat selection influence realized population connectivity?. – *Ecology* 93: 1378–1387.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. – Springer.

Careau, V. et al. 2008. Energy metabolism and animal personality. – *Oikos* 117: 641–653.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. – *Theoretical population biology* 14: 215–230.

Clobert, J. et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. – *Ecology letters* 12: 197–209.

Clutton-Brock, T. 2007. Sexual selection in males and females. – *Science* 318: 1882–1885.

Da Silva, A. et al. 2009. Heterozygosity-fitness correlations revealed by neutral and candidate gene markers in roe deer from a long-term study. – *Evolution: International Journal of Organic Evolution*, 63: 403-417.

de Kroon, H. et al. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. – *Ecology* 67: 1427–1431.

Debeffe, L. et al. 2012. Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. – *J. Anim. Ecol*. 81: 1327–1327.

Delattre, T. et al. 2013. Interactive effects of landscape and weather on dispersal. – *Oikos* 122: 1576–1585.

Dingemanse, N. J. et al. 2004. Fitness consequences of avian personalities in a fluctuating environment. – *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271: 847–852.

Dingemanse, N. J. et al. 2019. Individual variation in age-dependent reproduction: fast explorers live fast but senesce young?. – *Journal of Animal Ecology*.

Donaldson, J. R. et al. 2005. Competition-and resource-mediated tradeoffs between growth and defensive chemistry in trembling aspen (*Populus tremuloides*). – *New Phytologist* 169: 561–570.

Douhard, F. et al. 2017. The cost of growing large: costs of post-weaning growth on body mass senescence in a wild mammal. – *Oikos* 126: 1329–1338.

Festa-Bianchet, M. et al. 2000. Early development, adult mass, and reproductive success in bighorn sheep. – *Behavioral Ecology* 11: 633–639.

Gaillard, J. M. et al. 2000. Temporal variation in fitness components and population dynamics of large herbivores. – *Annual Review of ecology and Systematics* 31: 367–393.

Gaillard, J. M. et al. 2003. Cohort effects and deer population dynamics. – *Ecoscience* 10: 412–420.

Gaillard, J. M. et al. 2004. Assessing senescence patterns in populations of large mammals. – *Animal Biodiversity and Conservation* 27: 47–58.

Gaillard, J. M. et al. 2008. Population density and sex do not influence fine-scale natal dispersal in roe deer. – *Proceedings of the Royal Society B: Biological Sciences* 275: 2025–2030.

Gaillard, J. M. et al. 2013. How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. – *Ecology letters* 16: 48–57.

Hewison, A. J. M. et al. 1998. Social organisation of European roe deer. – In: Andersen, R. et al. (eds), *The European roe deer: the biology of success*. Scandinavian Univ. Press, Oslo, pp. 189–219.

Hewison, A. J. et al. 2009. Landscape fragmentation influences winter body mass of roe deer. – *Ecography* 32: 1062–1070.

IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Kirkwood, T. B. and Rose, M. R. 1991. Evolution of senescence: late survival sacrificed for reproduction. – *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 332: 15–24.

Lemaître, J. F. et al. 2015. Early-late life trade-offs and the evolution of ageing in the wild. – *Proceedings of the Royal Society B: Biological Sciences* 282: 20150209.

Linnell, J. D. and Andersen, R. 1998. Territorial fidelity and tenure in roe deer bucks. – *Acta Theriol*. 43: 67–75.

Massot, M. et al. 2008. Climate warming, dispersal inhibition and extinction risk. – *Global Change Biology* 14: 461–469.

Messina, F. J. and Slade, A. F. 1999. Expression of a life-history trade-off in a seed beetle depends on environmental context. – *Physiological Entomology* 24: 358–363.

Michel, E. S. et al. 2015. Contrasting the effects of maternal and behavioral characteristics on fawn birth mass in white-tailed deer. – *PloS one* 10: e0136034.

Monestier, C. et al. 2015. Is a proactive mum a good mum? A mother's coping style influences early fawn survival in roe deer. – *Behavioral Ecology* 26: 1395-1403.
Møller, A. P. et al. 2006. Dispersal and climate change: a case study of the Arctic tern Sterna paradisaea. – *Global Change Biology* 12: 2005–2013.

Montiglio, P. O. et al. 2018. The pace-of-life syndrome revisited: the role of ecological conditions and natural history on the slow-fast continuum. – *Behavioral ecology and sociobiology* 72: 116.

Murray, I. W., and Smith, F. A. 2012. Estimating the influence of the thermal environment on activity patterns of the desert woodrat (*Neotoma lepida*) using temperature chronologies. – *Canadian journal of zoology* 90: 1171-1180.

Nevoux, M. et al. 2013. The short-and long-term fitness consequences of natal dispersal in a wild bird population. – *Ecology letters* 16: 438–445.

Nilsen, E. B. et al. 2009. A slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer populations. – *Journal of Animal Ecology* 78: 585–594.

Nussey, D. H. et al. 2011. Patterns of body mass senescence and selective disappearance differ among three species of free-living ungulates. – *Ecology* 92: 1936–1947.

Pettorelli, N. et al. 2002. Variations in adult body mass in roe deer: the effects of population density at birth and of habitat quality. – *Proceedings of the Royal Society of London. Series B: Biological Sciences* 269: 747–753.

Pettorelli, N. et al. 2001. Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. – *Oecologia* 128: 400-405.

Plard, F. et al. 2014. Mismatch between birth date and vegetation phenology slows the demography of roe deer. – *PLoS biology* 12: e1001828.

R Core Team 2019. R: A language and environment for statistical computing. – R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Réale, D. et al. 2009. Male personality, life-history strategies and reproductive success in a promiscuous mammal. – *Journal of evolutionary biology* 22: 1599–1607.

Réale, D. et al. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. – *Philosophical Transactions of the Royal Society B: Biological Sciences* 365: 4051–4063.

Richards, S. A. 2008. Dealing with overdispersed count data in applied ecology. – *Journal of Applied Ecology* 45: 218–227.

Ripple, W. J. et al. 2019. World scientists' warning of a climate emergency. *BioScience*.

Robert, A. et al. 2012. The interaction between reproductive cost and individual quality is mediated by oceanic conditions in a long-lived bird. – *Ecology* 93: 1944-1952.

Schmid, M. et al. 2019. A tradeoff between robustness to environmental fluctuations and speed of evolution. – *bioRxiv*, 834234.

Searcy, C. A. et al. 2018. Positive correlation between dispersal and body size in Green Frogs (*Rana clamitans*) naturally colonizing an experimental landscape. – *Canadian Journal of Zoology* 96: 1378-1384.

Serrano Ferron, E. et al. 2012. Digestive plasticity as a response to woodland fragmentation in roe deer. – *Ecological Research* 27: 77-82.

Soulsbury, C. D. et al. 2008. Fitness costs of dispersal in red foxes (*Vulpes vulpes*). – *Behavioral Ecology and Sociobiology* 62: 1289–1298.

Stearns, S. C. 1989. Trade-offs in life-history evolution. – *Functional ecology* 3: 259–268.

Stevens, V. M. et al. 2012. How is dispersal integrated in life histories: a quantitative analysis using butterflies. – *Ecology letters* 15: 74–86.

Toïgo, C. et al. 2006. How does environmental variation influence body mass, body size, and body condition? Roe deer as a case study. – *Ecography* 29: 301-308.

Van de Pol, M. and Verhulst, S. 2006. Age-dependent traits: a new statistical model to separate within-and between-individual effects. – *The American Naturalist* 167: 766–773.

Van Noordwijk, A. J. and de Jong, G. 1986. Acquisition and Allocation of Resources - Their Influence on Variation in Life-History Tactics. *American Naturalist* 128:137–142.

Vanpé, C. et al. 2010. Assessing the intensity of sexual selection on male body mass and antler length in roe deer *Capreolus capreolus*: is bigger better in a weakly dimorphic species?. – *Oikos* 119: 1484-1492.

Vilà-Cabrera, A. et al. 2014. Variation in reproduction and growth in declining Scots pine populations. – *Perspectives in plant ecology, evolution and systematics* 16: 111–120.

Wauters, L. A. 1995. Do female roe deer in good condition produce more sons than daughters. – *Behavioral Ecology and Sociobiology* 37: 189-193.

Wilson, P. N. and Osbourn, D. F. 1960. Compensatory growth after undernutrition in mammals and birds. – *Biological reviews* 35: 324–361.

Wingfield, J. C. et al. 1998. Ecological bases of hormone—behavior interactions: the "emergency life history stage". – *American Zoologist* 38: 191-206.

Woodhams, D. C. et al. 2008. Life-history trade-offs influence disease in changing climates: strategies of an amphibian pathogen. – *Ecology* 89: 1627–1639.

Zani, P. A. 2008. Climate change trade-offs in the side-blotched lizard (*Uta stansburiana*): effects of growing-season length and mild temperatures on winter survival. – *Physiological and Biochemical Zoology* 81: 797–809.

Supplementary Materials

Annex I: Variations of growth in males

1. Variations in male growth with age

Table S1: Candidate generalized additive mixed models (gamm) describing male growth during their lives in relation to age. Age was described either as a continuous variable, as age classes (adult: 2 to 8 years old, senescent individual: > 8 years), using a threshold effect at ages from 8 to 12 or using a thin plate regression spline. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain two random effects (cohort and individual identity), but these are not mentioned in the table. Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
s(Age)	**150.95**	**1640.92**	**0.00**
Age continuous	127.35	1785.02	144.09
Threshold (9 years)	128.04	1798.69	157.77
Threshold (10 years)	128.10	1799.82	158.90
Threshold (8 years)	127.99	1799.82	158.90
Threshold (12 years)	127.65	1800.66	159.74
Threshold (11 years)	127.67	1800.74	159.82
Null	125.93	1802.15	161.22
Age class	124.60	1803.98	163.06

2. Variations in male growth with age and dispersal status

Table S2: Candidate gamm models describing male growth throughout their lives in relation to age and dispersal status. Age was described using a thin plate regression spline specific or not for each dispersal status. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain two random effects (cohort and individual identity), but these are not mentioned in the table. Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
S(age)	**151.73**	**1643.46**	**0.00**
S(age by status)	157.12	1657.93	14.47

3. Variations in male growth with dispersal status, period, sector quality, body mass and age

Table S3: Candidate gamm models describing variations in male growth from the juvenile stage across an individual's life in relation to age, body mass, dispersal status, period and sector quality. Age is modelled using a thin plate regression spline. The reference dispersal status is dispersers and the reference period is period 2. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain the effects of two random effects (cohort and individual identity), but these are not mentioned in the table. Retained model is highlighted in bold.

Models	df	AICc	ΔAICc
Body mass*period + age	**123.77**	**1329.76**	**0.00**
Body mass + status + period + age	124.05	1331.06	1.31
Body mass*period + sector + age	124.32	1331.46	1.70
Body mass*status*period + age	124.21	1331.54	1.78
Body mass*status*period + sector + age	124.82	1333.43	3.67
Body mass + period + age	124.99	1333.85	4.09
Body mass + status + age	124.93	1334.23	4.47
Body mass*status + age	125.46	1335.97	6.21
Body mass + age	126.13	1337.83	8.07
Body mass*status + sector + age	126.07	1337.93	8.17
Status + age	130.20	1351.07	21.31
Status + period + age	130.28	1351.32	21.56
Status*period + age	130.39	1351.54	21.79
Period + age	130.22	1352.08	22.32
Age	130.87	1353.24	23.48
Status*period + sector + age	130.92	1353.36	23.60
Sector + age	131.38	1354.96	25.20

4. Variations in male growth from juvenile to yearling stage

Table S4: Candidate gamm models describing variations in growth from the juvenile stage to the yearling stage in relation to body mass, dispersal status, period and sector quality. The reference dispersal status is philopatric individuals and the reference period is period 2. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain cohort modelled as a random effect but it is not mentioned in the table. Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
Period	**12.80**	**369.10**	**0**
Body mass + period	13.48	370.63	1.53
Period + status	15.10	370.65	1.55
Body mass + status + period + sector	16.37	370.66	1.56
Sector	15.81	370.84	1.74
Null model	14.93	372.41	3.31
Status	17.17	372.53	3.43
Status*period + sector	16.87	373.25	4.15
Body mass*period + sector	15.85	373.68	4.58
Body mass + status	18.74	374.79	5.69
Body mass	15.97	374.94	5.84
Body mass*status + sector	20.67	375.35	6.25
Body mass*status + status*period + sector	18.50	376.94	7.84
Body mass*status*period	20.82	385.78	16.68
Body mass*status*period + sector	21.76	386.76	17.66

Table S5: Summary statistics of the retained gamm model describing male growth from juvenile stage to the yearling stage in relation to period. We report parameter estimates (±SE), t values, and p-value. Significant effects are indicated in bold writing.

Parameter	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	6.95	0.41	16.80	< 0.001
Period 1	-1.02	0.74	-1.38	0.17
Period 3	**-1.55**	**0.53**	**-2.92**	**0.005**
Smooth effects :				
	edf	Ref.df	F	p-value
Random effect of cohort	**8.80**	**21.00**	**1.12**	**0.001**

5. Variations in male growth from yearling to adult stages

Table S6: Candidate gamm models describing variations in growth from the yearling stage to the adult stage in relation to body mass, dispersal status, period and sector quality. The reference dispersal status is philopatric individuals and the reference period is period 1. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain cohort modelled as a random effect (not mentioned in the table). Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
Sector	**4.57**	**150.42**	**0**
Null model	2.00	152.73	2.32
Body mass + period	5.00	152.85	2.44
Body mass	3.00	153.06	2.64
Period	4.00	153.13	2.71
Status	3.00	155.03	4.61
Body mass + status	4.00	155.13	4.72
Period + status	5.00	155.66	5.25
Body mass + status + period + sector	9.97	155.70	5.28
Body mass*status + sector	10.22	156.01	5.59
Body mass*period + sector	10.94	158.70	8.28
Status*period + sector	10.09	159.57	9.15
Body mass*status + status*period + sector	12.69	165.18	14.76
Body mass*status*period	13.00	177.96	27.54
Body mass*status*period + sector	17.30	183.01	32.59

Annex II: Variations of growth in females

1. Variations in female growth with age

Table S7: Candidate generalized additive mixed models (gamm) describing female growth throughout their lives in relation to age. Age was described either as a continuous variable, as age classes (adult: 2 to 12 years old, senescent individual: > 12 years), using a threshold effect at ages from 8 to 12 years old or using a thin plate regression spline. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain two random effects (cohort and individual identity), but these are not mentioned in the table. Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
S(age)	**152.63**	**2192.86**	**0.00**
Age (threshold at 10 years old)	140.87	2361.05	168.19
Age (threshold at 11 years old)	140.58	2361.44	168.58
Age (threshold at 12 years old)	140.22	2362.55	169.69
Age (threshold at 9 years old)	140.99	2363.36	170.50
Age (continuous)	137.17	2366.80	173.94
Age class	140.28	2368.07	175.21
Age (threshold at 8 years old)	140.78	2368.48	175.62
Null	137.68	2376.63	183.77

2. Variations in female growth with age and dispersal status

Table S8: Candidate gamm models describing female growth during their lives in relation to age and dispersal status. Age was described using a thin plate regression spline. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain two random effects (cohort and individual identity), but these are not mentioned in the table. Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
S(age)	**152.63**	**2192.86**	**0.00**
S(age) * status	155.74	2197.81	4.95

3. Variations in female growth with dispersal status, period, sector quality, age and body mass

Table S9: Candidate gamm models describing variations in female growth from the juvenile stage throughout their lives in relation to age, body mass, dispersal status, period and sector quality. Age is modelled using a thin plate regression spline. The reference dispersal status is dispersers and the reference period is period 1. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain the effect of two random effects (cohort and individual identity), but these are not mentioned in the table. Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
Body mass + period + age	**143.42**	**2173.21**	**0**
Body mass*period + age	143.75	2174.05	0.84
Body mass*period + sector + age	144.02	2174.47	1.26
Body mass*status*period + age	144.52	2175.1	1.89
S(age) + Body mass*status*period + sector + age	145.03	2175.94	2.73
Body mass + age	145.49	2177.3	4.09
Body mass*status + sector + age	145.72	2178.04	4.83
Body mass*status + age	146.01	2178.28	5.07
Body mass + status + age	146.04	2178.46	5.25
Status + period + age	151.5	2191.52	18.31
Period + age	152.61	2192.18	18.97
Status*period + sector + age	152.41	2192.34	19.13
Status*period + age	152.69	2192.69	19.48
Age	152.63	2192.86	19.65
Sector + age	152.67	2192.88	19.67
Status + age	153.27	2193.9	20.69

4. Variations in female growth from juvenile to yearling stage

Table S10: Candidate generalized additive mixed effect models (gamm) describing variations in female growth from the juvenile stage to the yearling stage in relation to body mass, dispersal status, period and sector quality. The reference dispersal status is dispersers and the reference period is period 2. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain cohort modelled as a random effect but it is not mentioned in the table. Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
Body mass + period	**17.52**	**354.38**	**0**
Body mass	18.65	357.3	2.92
Period	16.85	357.38	3
Null model	16.83	357.46	3.08
Sector	17.38	358.35	3.97
Body mass + status+ period+sector	19.27	359.95	5.57
Period+status	17.91	360.54	6.16
Status	17.69	360.84	6.46
Body mass + status	19.5	360.88	6.5
Body mass*period + sector	19.84	361.92	7.54
Body mass*status + sector	20.44	365.05	10.67
Status*period + sector	19.91	365.73	11.35
Body mass*status+status*period+sector	21.31	366.82	12.44
Body mass*status*period	23.86	373.11	18.73
Body mass*status*period + sector	24.72	376.3	21.92

5. Variations in female growth from yearling to adult stage

Table S11: Candidate gamm models describing variations in female growth from the yearling to the adult stage in relation to juvenile body mass, dispersal status, period and sector quality. The reference dispersal status is dispersers and the reference period is period 1. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain cohort modelled as a random effect (not mentioned in the table). Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
Body mass + period	**7.97**	**215.45**	**0**
Body mass	8.49	216.91	1.46
Period	4.08	218.15	2.7
Body mass + status+period+sector	9.37	219.07	3.62
Body mass + status	9.03	219.13	3.68
Period+ sector	5	219.65	4.2
Body mass*period + sector	10.36	222.23	6.78
Body mass*status + sector	10.29	222.9	7.45
Body mass*status+status*period+sector	12.07	226.17	10.72
Status*period + sector	8	226.67	11.22
Null model	11.66	231.68	16.23
Sector	10.22	232.37	16.92
Sector	12.42	234.11	18.66
Body mass*status*period	14.77	234.36	18.91
Body mass*status*period + sector	15.69	237.65	22.2

6. Variations in female growth from adult to senescent stages

Table S12: Candidate gamm models describing variations in female growth from the adult stage to the senescent stage in relation to body mass, dispersal status, period and sector quality. The reference dispersal status is philopatric individuals and the reference period is period 1. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain cohort modelled as a random effect but it is not mentioned in the table. Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
Body mass + status	**9.16**	**68.49**	**0**
Period	9.42	78.45	9.96
Null model	9.75	95.28	26.79
Status	10.39	140.02	71.53
Sector	10.37	148.38	79.89
Body mass	10.68	191.77	123.28

Annex III: Reproductive Success

1. Probability to reproduce

A- Effect of age on the probability to reproduce during all life

1) Effects of age and dispersal status on the probability to reproduce throughout life

Table S13: Candidate generalized additive mixed effect models (gamm) describing the propensity of females to reproduce during their lives in relation to age. Age was described either as a continuous variable, as age classes (adult: 2 to 12 years old, senescent individual: > 12 years), using a threshold effect at ages from 9 to 12 years old, or using a thin plate regression spline. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain two random effects (cohort and individual identity), but these are not mentioned in the table. Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
Age(threshold at 10 years old)	**33.27**	**384.17**	**0**
Age(threshold at 11 years old)	32.69	385.13	0.96
S(age)	35.25	387.76	3.59
Age(threshold at 9 years old)	33.26	388.11	3.94
Age(threshold at 12 years old)	30.95	388.94	4.77
Age(threshold at 8 years old)	34.29	392.65	8.48
Age class	34.78	406.35	22.18
Age (continuous)	35.55	420.13	35.96

Table S14: Candidate generalised linear mixed models (glmer) describing the propensity of females to reproduce throughout their lives in relation to age, dispersal status and body mass. Age was described using a threshold effect at 10 years old. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain two random effects (cohort and individual identity), but these are not mentioned in the table. Retained models are highlighted in bold.

Model	df	AICc	ΔAICc
Age (threshold at 10 years old) * status + body mass	**7**	**375.55**	**0.00**
Age (threshold at 10 years old) + body mass	**5**	**377.19**	**1.64**

Table S15: Summary statistics of the retained glmer model describing female propensity to reproduce throughout its life in relation to body mass, age and dispersal status. We report parameter estimates (±SE) for each variable that featured in the retained models, z values, and p-value. Significant effects are indicated in bold writing.

Parameters	Estimate	Std. Error	Adjusted SE	Z values	p-value
(Intercept)	-3.68	1.69	1.70	2.17	0.03
Age (Threshold at 10 years old)	**-0.93**	**0.17**	**0.17**	**5.44**	**< 0.001**
Status Philopatric individual	0.72	0.42	0.42	1.69	0.09
Body mass	**0.29**	**0.07**	**0.07**	**3.95**	**< 0.001**
Status Philopatric individual:Age (Threshold at 10 years old)	0.21	0.28	0.28	0.75	0.45

2) Effets of dispersal status, period, sector, body mass and age on the probability to reproduce throughout life

Table S16: Candidate generalized linear mixed effects models (glmer) describing the propensity of females to reproduce throughout their lives in relation to dispersal status, body mass, period, sector and age. Age was described using a threshold effect at 10 years old. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain the effect of age and two random effects (cohort and individual identity), but these are not mentioned in the table. Retained model is highlighted in bold.

Model	df	AIC	ΔAICc
Status*body mass + age	**7**	**370.01**	**0.00**
Status*body mass + sector + age	8	371.54	1.53
Status*period + Status*body mass + age	11	377.08	7.07
Body mass + age	5	377.10	7.10
Status*period + status*body mass + sector + age	12	378.39	8.38
Age	4	391.69	21.68
Sector + age	5	392.91	22.91
Dispersal status + age	5	393.30	23.29
Period + age	6	393.41	23.41
Status*period + age	9	396.73	26.72
Status*period+sector + age	10	397.60	27.59

B. Probability to reproduce at two years old

Table S17: Candidate generalized linear mixed effects models (glmer) describing the propensity of females to reproduce at two years old in relation to dispersal status, body mass, period and sector. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain the random effects of cohort, but it is not mentioned in the table. Retained model is highlighted in bold.

Models	df	AICc	ΔAICc
Body mass	**3**	**69.89789**	**0**
Status*body mass + sector	6	70.07834	0.18045
Status*body mass	5	70.11851	0.22062
Status + body mass	4	70.20603	0.30814
Status*period+ status*body mass	9	70.66514	0.76725
Status*period+ status*body mass + sector	10	72.42094	2.52305
Null	2	74.33492	4.43703
Sector	3	75.50816	5.61027
Status	3	76.43309	6.5352
Period	4	76.91469	7.0168
Status*period	7	79.82072	9.92283

B- Probability to get more than one embryo

a. During the entire life

Table S18: Candidate generalized additive mixed models (gamm) describing the propensity of females to have more than one embryo during their lives in relation to age. Age was described either as a continuous variable, as age classes (adult: 2 to 12 years old, senescent individual: > 12 years), using a threshold effect at ages from 9 to 12 years old or using a thin plate regression spline. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contained two random effects (cohort and the identity of the individual). Retained model is highlighted in bold.

Model	df	AICc	ΔAICc
s(age)	**63.86**	**711.79**	**0.00**
Threashold 8 years	63.84	728.74	16.95
Threashold 9 years	63.06	728.93	17.14
Threashold 10 years	61.80	729.50	17.71
Age class	61.54	729.80	18.02
Threashold 11 years	60.77	732.39	20.60
Threashold 12 years	60.80	734.95	23.16
Age (continuous)	60.77	735.13	23.35

Table S19: Candidate gamm models describing the propensity of females to have more than one embryo throughout their lives in relation to age, dispersal status and body mass. Age was described using a thin plate regression spline. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain two random effects (cohort and individual identity), but these are not mentioned in the table. Retained models are highlighted in bold. The result from the model averaging procedure indicates a significant effect of age for two different dispersal statuses and a significant effect of body mass.

Model	df	AICc	ΔAICc
S(age, by status) + masse	**43.05**	**633.70**	**0**
S(age)+ masse	**39.38**	**634.800**	**1.1**

Table S20: Candidate gamm models describing the propensity of females to have more than one embryo throughout their lives in relation to age, dispersal status, body mass, period and sector. Age was described using a thin plate regression spline specific for each dispersal status. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). All models contain the effect of age and two random effects (cohort and individual identity), but these are not mentioned in the table. Retained model is highlighted in bold.

Models	df	AICc	ΔAICc
Body mass + age	**43.04602**	**633.7043**	**0**
Status*body mass + sector + age	46.54082	635.1439	1.4396
Status + body mass + age	44.91365	635.7777	2.0734
Status*period+ status*body mass + sector + age	51.24822	639.0104	5.3061
Status*period+ status*body mass + age	51.80841	639.9376	6.2333
Period + age	46.70191	695.8747	62.1704
Status*period + age	51.07638	700.686	66.9817
Status*period + esta + age	52.37804	701.9938	68.2895
Age	67.2195	709.6116	75.9073
Sector + age	68.58267	710.7835	77.0792
Status + age	68.76316	711.6619	77.9576

b. At two years old

Table S21: Candidate gamm model describing the propensity of females to have more than one embryo at two years old in relation to dispersal status, period, body mass sector and age. All models included age modelled using a thin plate regression spline and cohort modelled as a random effect, but they were not mentioned in the table. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df). Retained models are highlighted in bold.

Models	df	AICc	ΔAICc
Body mass + sector	**4**	**61.86828**	**0**
Body mass	**3**	**63.22671**	**1.35843**
Body mass + status + sector	5	63.55179	1.68351
Status + body mass	4	64.36019	2.49191
Status*body mass + sector	6	65.86088	3.9926
Status*body mass	5	66.62336	4.75508
Status*period + status*body mass	7	70.73021	8.86193
Status + period + sector	5	84.67934	22.81106
Status*period	5	86.7976	24.92932
Status*period + status*body mass + sector	6	86.96442	25.09614
Status*period + sector	6	86.96442	25.09614
Period	3	88.20197	26.33369
Status	3	95.66527	33.79699
Null	2	103.38883	41.52055
Sector	3	103.95216	42.08388

Chapter III:

Beyond dispersal versus philopatry?

Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape

OIKOS

SYNTHESISING ECOLOGY

Volume 129 • January 2020

Photo by Bruno Lourtet

OIKOS

Research

Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape

Delphine Ducros, Nicolas Morellet, Rémi Patin, Kamal Atmeh, Lucie Debeffe, Bruno Cargnelutti, Yannick Chaval, Bruno Lourtet, Aurélie Coulon and A. J. Mark Hewison

D. Ducros (https://orcid.org/0000-0002-3227-7085) (ducros.delphine@gmail.com) and A. Coulon (https://orcid.org/0000-0003-0309-2214), Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Univ., CP 135, 57 rue Cuvier, FR-75005 Paris, France. – DD, N. Morellet (https://orcid.org/0000-0002-4274-7044), L. Debeffe, B. Cargnelutti, Y. Chaval, B. Lourtet and A. J. M. Hewison (https://orcid.org/0000-0002-2276-4154), CEFS, Univ. de Toulouse, INRA, Castanet-Tolosan, France. – AC and R. Patin (https://orcid.org/0000-0002-4448-2844), CEFE, CNRS, Univ. Montpellier, EPHE, IRD, Montpellier, France. – K. Atmeh (https://orcid.org/0000-0002-0564-8821), Laboratoire de Biométrie et Biologie Evolutive (LBBE), Univ. Lyon, CNRS, Villeurbanne, France.

Oikos
00: 1–12, 2019
doi: 10.1111/oik.06793

Subject Editor and
Editor-in-Chief: Dries Bonte
Accepted 1 September 2019

Although inter-individual heterogeneity in many aspects of dispersal behaviour is widely reported, this key life-history trait is predominantly modelled as a dichotomous state of philopatry versus dispersal. The increasing body of evidence for dispersal syndromes (i.e. a suite of correlated morphological, behavioural and life-history traits associated with dispersal) implies substantial but, to date, undocumented individual heterogeneity in behavioural tactics during dispersal. Using a large sample (n = 154) of GPS monitored juvenile roe deer *Capreolus capreolus*, we evaluated among-individual behavioural heterogeneity in dispersal tactics, and the individual and environmental drivers of these alternative tactics. We developed a sequential three-stage decision tree based on space use stability, exploration events and the directionality of movement. We identified six discrete alternative behavioural tactics during the dispersal period which were characterised by different timing, amplitude and duration in movement: slightly less than half of the deer were sedentary, either 'strictly philopatric' or 'explorers', which subsequently settled on their natal range; around 40% dispersed ('classic dispersal'), of which, one in six subsequently aborted, moving back to their natal range ('aborted dispersal'); finally, around 15% expressed either a 'progressive dispersal' tactic, gradually moving away from their natal area to settle elsewhere, or a 'multi-range' tactic. The propensity to express an alternative dispersal tactic was strongly influenced by an individual's local environment. In particular, when landscape heterogeneity, resource quality and human-related disturbance in the natal range were low, individuals were 1) more likely to adopt the alternative tactics of either progressive dispersal or multi-ranging, but 2) also more likely to abort their dispersal attempt. Our work indicates that natal dispersal is likely not a single uniform behaviour, but that individuals may adopt a variety of alternative movement tactics which are likely governed by different selection pressures, with potentially important impacts for population dynamics and functioning.

Keywords: directionality, exploration, GPS, movement ecology, natal range, ungulate

NORDIC SOCIETY OIKOS

www.oikosjournal.org

Introduction

Dispersal describes any movement of an organism which may impact gene flow through space (Ronce 2007), with far-reaching consequences for many biological processes such as population structuring, biological invasions and species adaptation (Ronce 2007, Clobert et al. 2012). However, while there is now a solid theoretical and empirical underpinning to current knowledge on dispersal (Holyoak et al. 2008, Gibbs et al. 2010, Clobert et al. 2012, Fronhofer et al. 2018), empirical studies describing the diversity of dispersal-related movement behaviours in the wild remain relatively scarce (but see Debeffe et al. 2012, Mayer et al. 2017 for recent examples). In particular, over the last two decades, a growing body of literature has demonstrated that dispersal is a highly heterogeneous process (Bowler and Benton 2005, Fronhofer et al. 2018), comprising three phases, emigration, transience and settlement. Experimental and empirical approaches have demonstrated marked heterogeneity among individuals in, for example, the propensity (Bonte et al. 2003) and timing (Mayer et al. 2017) of emigration, the duration of dispersal transience (Rémy et al. 2011) and habitat selection during settlement (Haughland and Larsen 2004). Indeed, individuals may adjust their dispersal decisions plastically in relation to a variety of environmental factors (Bonte et al. 2006, 2008, Jacob et al. 2016). For instance, the quality of the natal environment may impact the ability of an individual to establish its post-dispersal range (Stamps 2006) and should therefore influence its decision whether or not to disperse. Indeed, informed dispersal in relation to seasonality and environmental conditions is likely widespread in animals (Clobert et al. 2009).

In some species, development of specific morphological and/or physiological specializations is required to successfully disperse, generating discrete disperser and non-disperser phenotypes (Braendle et al. 2006, Martorell and Martinez-Lopez 2014). Because dispersal syndromes (covariation among morphological and/or behavioural traits) appear to be widespread (Clobert et al. 2009, Ronce and Clobert 2012), individuals may also express discrete alternative behavioural tactics during dispersal (Doerr and Doerr 2005, Clobert et al. 2009). By alternative tactics, we mean the set of alternative behaviours an individual may potentially express in response to a given environmental context. For example, Bonte et al. (2008) showed that individual spiders can disperse through either ballooning or rappelling depending on thermal conditions during development, while alternative amphidromous and non-amphidromous dispersal tactics were identified in the goby *Awaous stamineus* (Hogan et al. 2014). These alternative tactics likely incur different costs: for example, increasing dispersal distance can increase mortality costs (Stamps et al. 2005), while energy costs are likely higher for dispersing individuals that do not successfully settle in their post-dispersal range and must return to their natal range (Maag et al. 2019). However, despite the potential impact of these costs for the evolution of dispersal, no study has yet investigated alternative behavioural tactics across the phases of the dispersal process. This is, without doubt, in part due to the logistical challenge of recording detailed behaviour in the wild. Indeed, dispersing individuals may move rapidly through the landscape, often cryptically and potentially at night, so that direct observation is impossible. For sufficiently large species, remote monitoring by, for example, animal borne GPS devices provides the opportunity to track dispersal movements and behaviours in a precise way (Kays et al. 2015). However, there are, as yet, very few studies that have amassed sufficient data to address this question in a natural setting and, hence, dispersal is still invariably modelled as a dichotomous state of philopatry versus dispersal (Torrents-Tico et al. 2018).

Here, we exploited a long-term dataset on a wild population of roe deer *Capreolus capreolus* inhabiting a heterogeneous landscape in the south of France to investigate 1) inter-individual heterogeneity in dispersal behaviour and 2) the individual and environmental drivers of these alternative tactics. We collected precise information on the spatial behaviour of a large sample (n = 154) of juvenile roe deer using intensive GPS tracking during the period of dispersal and coupled it with detailed data on landscape structure and individual phenotype. Dispersal in roe deer occurs at around 1 year of age, between the end of March and May (Debeffe et al. 2012), and is equally prevalent in both sexes (Coulon et al. 2006, Gaillard et al. 2008). Subsequently, most individuals remain faithful to their settlement range for their entire life (Linnell and Andersen 1998, Hewison et al. 1998). Although there is substantial published baseline information in this species (Wahlström and Liberg 1995, Coulon et al. 2004, Vanpé et al. 2016), as elsewhere, dispersal and philopatry were considered as the sole alternative behavioural states (but see Van Moorter et al. 2008, Debeffe et al. 2013 on pre-dispersal exploration behaviour). Thus, in a first step, we developed a method to classify individuals in terms of alternative dispersal tactics based on the spatial distribution, directionality and duration of their movements in relation to their presumed natal range. Subsequently, we investigated how individuals that were assigned to these novel alternative behavioural tactics differed in terms of their phenotype and their natal environment. In particular, we expected that the propensity of an individual to express a given tactic would depend on the characteristics of its natal range in terms of the availability of crops and meadows for feeding, the level of anthropogenic disturbance and landscape heterogeneity.

Material and methods

Study area

The roe deer population inhabits a heterogeneous landscape of ca 19 000 ha in southwest France (43°13′N, 0°52′E) composed of 36% crops (e.g. alfalfa, wheat, barley, sunflower, corn, soya, sorghum and rape), 31% meadows, 18% small oak-dominated (*Quercus* spp.) woodland patches and hedges, and two large forests of 672 and 515 ha

(see Martin et al. 2018 for more details). Human presence is high, with villages, isolated houses and farms, and an extensive (2.15 km km^{-2}) secondary road network all widely distributed. Drive hunts with dogs occur on a regular basis from September to February and stalking from June to August. Roe deer density was estimated using a capture–mark–resighting approach at ca 10 deer per 100 ha in the more open areas of the landscape, and two to three times higher in the forest massifs (Hewison et al. 2007). The climate is oceanic, with an average temperature of 11–12°C and 800 mm precipitation per year, mostly rain.

Roe deer monitoring

Capture events occurred during winter from 2002 to 2017, on 11 different sites, using net drives with about 30–100 beaters and catchers placed regularly along a 4 km net line. When caught, roe deer were tranquilised using an intramuscular injection of acepromazine (0.075 mg kg^{-1}), and placed in a wooden retention box to prevent stress and injury prior to marking (for more details of the capture procedure, see Morellet et al. 2009). For each animal, we recorded sex, body mass and age class. Juveniles (8–10 months old) were distinguished from older deer based on the presence of a tricuspid third pre-molar milk tooth (Ratcliffe and Mayle 1992). To record their natal dispersal behaviour, juveniles were then equipped with a GPS collar, some of which also provided remote data transmission. Collars were programmed to record a GPS location every 4 h for the first two years of the study, and every 6 h subsequently, over a period of approximately 11 months. In total, we obtained GPS records for 170 juveniles since 2002. We removed the first seven days of monitoring, when behavioural alterations due to capture and handling may be pronounced (Morellet et al. 2009), prior to analyses. We then performed differential correction to improve fix accuracy (Adrados et al. 2003) and eliminated obviously erroneous locations (0.0003% of the total dataset). Once we had removed individuals that experienced collar dysfunction or mortality events during the first seven days of monitoring, we obtained a final sample of 154 juveniles for analysis.

Classification method and criteria

Our central objective was to analyse inter-individual variation in movement behaviour in order to characterise alternative movement tactics during the process of natal dispersal. Based on current knowledge of dispersal ecology, we identified home range stability, exploration movements and directionality as informative criteria that are generally used to characterise dispersal (Haughland and Larsen 2004, VanderWaal et al. 2009, Elliot et al. 2014). To classify individuals, we first investigated clustering methods such as the K-nearest neighbours method (Mucherino et al. 2009) and random forest analysis (Breiman 2001). However, the order in which these criteria are implemented is critical to differentiate alternative tactics, such that the value taken by one criterion depends on the value of the criterion implemented at the previous step. This involves a step-by-step calculation of variables, which is difficult to implement in a classic clustering approach. We hence elaborated a biologically-informed and unsupervised classification method based on current knowledge with respect to home range stability, exploration events and movement directionality. First, to distinguish small-scale, within-range movements linked to foraging activity from larger-scale movements outside of the usual home range, we segmented the time-series of GPS locations (x- and y-coordinates) for each individual using Lavielle's method (1999) originally developed for a one-dimensional variable, but recently adapted by Patin et al. (2019) to handle bi-dimensional data (R package segclust2d). This approach detects significant change points in a time series (here, the geographical coordinates of locations of an individual) which we used to identify spatio–temporal units corresponding to distinct ranges occupied successively by that individual, and linked by inter-range transitional movements. To provide enough flexibility for identifying alternative movement behaviours, we set the maximum number of segments to 15 and the minimum duration of each segment to 42 h (i.e. 7 inter-fix intervals of 6 h). However, in practice, we considered that a given segment corresponded to a distinct range when the individual's residence time in that segment lasted at least seven days (i.e. a minimum of 28 locations, see Couriot et al. 2018). Residence time (i.e. the total time spent by an individual in a given area, Barraquand and Benhamou 2008) for a given segment was estimated as the average time spent within a radius of 500 m (the average size of a roe deer home range at a monthly scale in this study area, Morellet et al. 2013) over all locations of that segment (using the R package 'recurse', Bracis et al. 2018). Because juvenile roe deer which were caught and monitored from their first winter are very unlikely to have already dispersed (Debeffe et al. 2012), and since migratory behaviour is negligible in our study population, the first segment of the time series that corresponded to a range was considered to be the natal range of that individual. Similarly, as GPS monitoring ceased in late autumn, we assumed that the last range identified from the time series represented the settlement range, since roe deer have been widely reported to occupy a stable adult range from 15 months of age onwards (Debeffe et al. 2012), with a very high level of site fidelity thereafter (Hewison et al. 1998). To illustrate this high spatial fidelity in our study system, we quantified the degree of overlap in locations of those individuals for which we had spatial information that covered several years. For individuals that were VHF- or GPS-monitored over at least two years during their lifetime, we measured range overlap using 50% fixed kernels between the post-dispersal range and the adult range, or between two subsequent adult ranges (libraries 'adehabitatHR', Calenge 2006 and 'rgeos', Bivand and Rundel 2017). For those that were monitored for one year only, but were subsequently recovered when they died, we compared their location at death to their locations during the monitoring period. When location at death or the adult range

overlapped with the post-settlement range or the adult range in a previous year, we considered the animal to be faithful to its home range. Firstly, of the 58 adults that were monitored during two or more years, 54 (~93%) were faithful to their core home range. Second, of the 30 juveniles that were monitored by GPS during the post-dispersal phase, 28 (~93%) were subsequently located within their settlement range during adulthood (see Supplementary material Appendix 1 for more details). Thus, the vast majority of individuals remained where they settled after the dispersal phase, irrespective of whether they dispersed or not, and hence most likely reproduced on their settlement range. Note, however, that some roe deer females may perform reproductive excursions during the rut, outside of their usual home range, presumably to mate with unrelated males (Debeffe et al. 2014). Finally, to identify alternative movement tactics during the dispersal period, we analysed the time series of ranges and inter-range movements for each individual using a sequential three-stage decision tree (Fig. 1).

Step 1. Did the individual use spatially-separate ranges?

By definition, dispersal occurs when an individual leaves its natal range and moves away to settle in a post-dispersal settlement range which is spatially distinct from the natal range and where reproduction potentially occurs (Kenward et al. 2002, Ronce 2007). Therefore, as a first step, we measured the degree of overlap between the natal and settlement ranges. Ranges were estimated using fixed-kernel methods and an ad hoc approach to select the optimal smoothing parameter with the 'adehabitatHR' package (Calenge 2006) for R. We measured the overlap at two spatial scales with the 'rgeos' package (Bivand and Rundel 2017): using the 50% fixed-kernel, which corresponds to the core area of the home range, and the 90% fixed-kernel, which corresponds to the estimated usual home range, hereafter named usual range (Worton 1989, Börger et al. 2006). When core areas of the natal and settlement ranges overlapped, the individual was assigned to one of the philopatric categories (see Step 2), whereas when both the core areas and usual ranges did not overlap, the individual was assigned to the 'classic disperser' tactic. When the core areas did not overlap, but the usual ranges did, we considered that these individuals were unusually mobile to conform to a strict definition of philopatry and, hence, required further investigation (see Step 3).

Step 2. Did the individual explore?

Because exploration is a common behaviour which may allow juveniles to assess the potential costs and benefits of dispersing (Clobert et al. 2009), in a second step, we investigated whether those individuals considered as philopatric above were, indeed, strictly sedentary ('strict philopatric' tactic) or whether they had explored the surrounding environment prior to settling on their natal range. To avoid confounding exploration with GPS error (Börger et al. 2006), we considered that an exploration event occurred if at least two successive fixes (i.e. incorporating an inter-fix interval of 6h) were situated outside an individual's usual range (Debeffe et al. 2013). Then, to distinguish between individuals that performed short term movements to explore their surrounding environment ('explorer' tactic), but that were essentially philopatric, from those that actually left their natal range to settle temporarily in a new range, before aborting the dispersal attempt and returning to their natal range ('aborted disperser' tactic), we calculated the residence time associated with the exploration event. Because pre-dispersal exploration

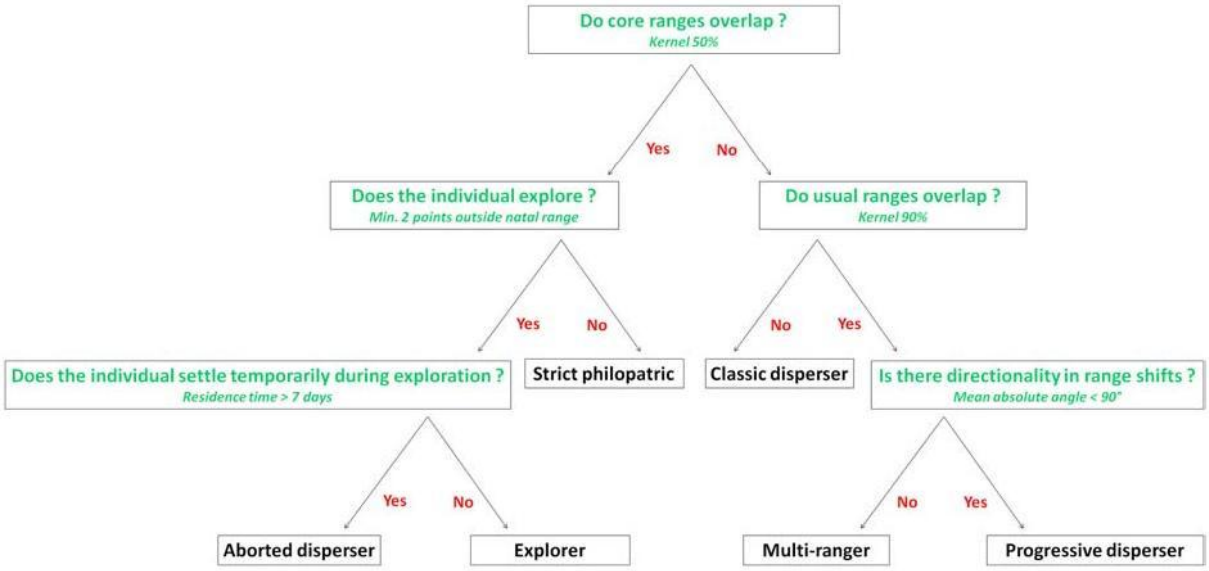


Figure 1. Classification steps to discriminate between alternative movement tactics of juvenile roe deer during the dispersal phase. The classification criteria are given in green, the dichotomous alternatives are in red and the six behavioural tactics identified with this decision tree are in black.

events in juvenile roe deer typically last around 24 h and never more than six days (Debeffe et al. 2013), we considered that a residence time of seven days or more indicated temporary settlement and, hence, the individual was classified as an aborted disperser.

Step 3. Did the individual shift its range in a consistent direction?

Although dispersal is often envisaged as an abrupt shift in spatial location (Greenwood 1980), it may not always include a clearly defined transience stage. Thus, in the third step of our classification, for individuals that were identified as unusually mobile above (see Step 1), we distinguished individuals that gradually moved away from their natal area in a consistent direction during a protracted dispersal transience phase ('progressive disperser' tactic) from individuals that moved periodically among different seasonal sub-ranges ('multi-range' tactic sensu Couriot et al. 2018). To do so, for all mobile individuals whose trajectory included at least three segments, we analysed directionality in their movement paths; that is, we measured the successive relative angles between the centroid of each segment using the package 'adehabitatLT' (Calenge 2006) and calculated the mean of the absolute angle values for each individual. With respect to the straight line that connected the centroids of the first two segments, we considered that the individual expressed directional persistence when the mean angle was less than 90°, so that the Euclidian distance from the natal area sequentially increased ('progressive disperser' tactic). Alternatively, a mean angle greater than 90° indicated that the animal moved back towards its initial location (i.e. the natal area), and therefore expressed a 'multi-range' tactic. Note that we could not evaluate directionality for individuals that only occupied two ranges. Because the multi-range tactic is a way to track seasonal fluctuations in resource distribution, and hence generally encompasses more than two sub-ranges within a given season (Couriot et al. 2018), we considered that these individuals were also 'progressive dispersers' (50% of the progressive dispersal class).

Drivers of alternative dispersal tactics

To identify the potential individual and environmental drivers of the alternative dispersal tactics identified above, we analysed the propensity for a juvenile roe deer to adopt a given tactic in relation to its sex, its body mass at capture and the habitat characteristics of its natal range. More precisely, we generated three landscape descriptors that were shown to affect dispersal behaviour in previous studies (Matthysen 2012, Fey et al. 2016): 1) we used the proportion of crops and meadows in the natal range to index nutritional quality of that range, as these habitats provide high quality resources for roe deer (Hewison et al. 2009); 2) to index landscape heterogeneity, we calculated the Shannon index based on the proportions of different habitat types within the natal range; 3) to index human-related disturbance, we calculated the distance to the nearest anthropogenic feature (road or building) in the natal range. In order to control for inter-individual variation in natal range size, we estimated these landscape descriptors for each individual within a standardised buffer of 98 ha (which corresponds to the average size of a natal range in our dataset) centred on the geometric centroid of the individual's natal range. We calculated the three landscape descriptors based on 10 000 randomly sampled locations within each buffer. We characterised local landscape composition in terms of land cover types with ArcGIS 10 (ESRI 2018) using a geographical information system in which all land cover polygons were manually digitized, based on aerial photographs, and described each summer using 41 land cover categories through field observation (for more details, see Morellet et al. 2011). For each random location, we recorded land use information for the year during which the individual was monitored, and we averaged all land use information obtained for the 10 000 locations in order to extract individual mean values for each landscape descriptor. Given the high level of co-linearity among the landscape descriptors, we first performed a principal component analysis (PCA) with varimax rotation to generate two or more independent (orthogonal) variables that described among-individual variation in landscape structure of the natal range (library 'ade4', Bougeard and Dray 2018). The three descriptors were scaled and centred prior to the PCA. We then used the principal components of the PCA that explained the most variation to analyse the relationship between landscape structure in the natal range and the propensity to adopt a given movement tactic.

We analysed alternative dispersal tactics one by one (relative to a reference dispersal tactic) as separate binary response variables and used generalized linear models with a logit link function (library 'stats', <www.r-project.org>) to analyse the propensity of an individual to adopt a specific movement tactic. More precisely, compared to classical dispersal, we evaluated the hypotheses that 1) the propensity to adopt an alternative dispersal tactic and 2) the propensity to abort a dispersal attempt would depend on the characteristics of an individual's natal range in terms of availability of crops and meadows, level of anthropogenic disturbance and landscape heterogeneity. To evaluate the above hypotheses, we first built a reference model including body mass (one individual was removed from this analysis because we had no body mass data for it), sex, their interaction (because the drivers of condition-dependent dispersal are likely sex-specific (Hewison et al. unpubl.) and the principal components of the landscape descriptors. Then, we compared a set of candidate models which comprised our reference model and all simpler nested models, including the constant model. Initially, we investigated both linear and non-linear effects of body mass using sex-specific thin plate regression splines. However, because in all cases linear models provided better fit to the data, we present only these results. We based our model selection on Akaike's information criterion corrected for small sample size (AICc, Burnham and Anderson 2002) and performed model averaging on all models within a ΔAICc of 2 of the best

model (library 'MuMIn', Barton 2018). For each model, we calculated Cook's distances to evaluate whether any observations might have a disproportionate influence on our results (library 'base'). Replicating the analyses after removing two such influential observations showed that model selection was robust to the inclusion of these points (results not shown). We used a binomial approach because it was better aligned with the structure of our hypotheses, but note that we obtained very similar results using multinomial models to evaluate the effect of landscape structure and phenotype on the six dispersal tactics simultaneously (library 'nnet', Venables and Ripley 2002; see Supplementary material Appendix 2 Table A6, A7). Statistical analyses were performed using the R software ver. 3.3.2 (<www.r-project.org>).

Data availability

The dataset analysed in this study is available from EURODEER (<https://eurodeer.org/>) upon request, and from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3s41j61> (Ducros et al. 2019).

Results

Identifying alternative movement tactics

Using our classification decision tree, we assigned 147 (68 males, 79 females) of the 154 juvenile roe deer to one of the six alternative movement tactics during the period of dispersal (Fig. 2; see Supplementary material Fig. A2 for more examples of individual trajectories). The remaining seven individuals could not be assigned to any behavioural tactic, either because we obtained too few GPS locations after initial data processing (n = 3), or because the animal moved erratically immediately after the capture event so that we were unable to identify the natal range (n = 4). Most individuals were either classified as classic dispersers, with a clear and well-defined transience stage (n = 49; 30 females and 19 males), or explorers, which only left their initial range for short periods of time and subsequently settled on their natal range (n = 62; 32 females and 30 males). Otherwise, 14 individuals were classified as progressive dispersers which gradually moved away from their natal area to settle elsewhere (5 females and 9 males), whereas 9 were classified as aborted dispersers which temporarily settled in a novel range, but moved back to settle in their natal range (5 females and 4 males). Finally, 9 individuals were assigned to the multi-range tactic (4 females and 5 males), while only 4 were strictly philopatric, never leaving their natal range (3 females and 1 male). For subsequent analyses, we therefore pooled these strictly philopatric individuals with the explorers as a single 'philopatric' class.

Using the bi-dimensional adaptation of Lavielle's segmentation approach, the movement paths comprised, on average, 2.3 (SD ± 1.2) segments (range 1–7 segments) per individual, lasting between 2 and 320 days. Except for the first segment which lasted, on average, 76.2 ± 38.9 days, there was pronounced variation in segment duration, both among segments and among classes (Supplementary material

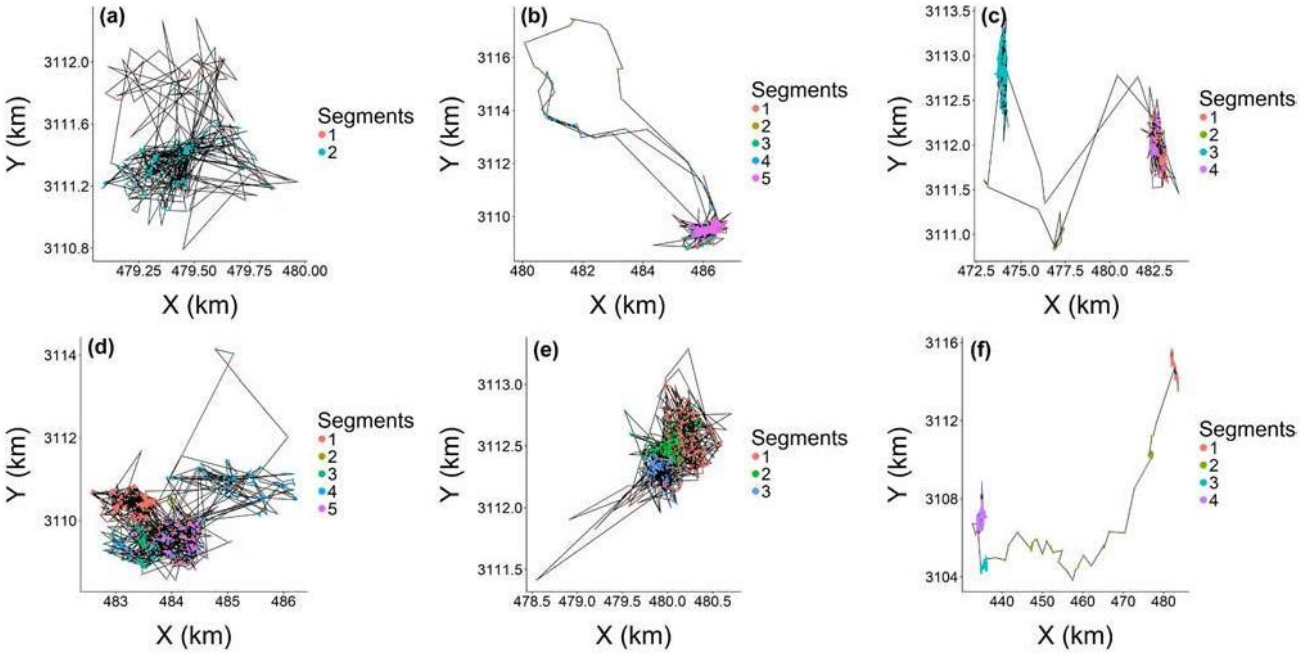


Figure 2. Examples of the six alternative movement tactics exhibited by juvenile roe deer during the dispersal phase: (a) strict philopatric; (b) explorer; (c) aborted disperser; (d) multi-ranger; (e) progressive disperser; (f) classic disperser. Each dot represents a GPS location, successive locations are linked by a straight line. Successive segments identified by the segmentation approach are coded in different colours and numbered chronologically. Latitude and longitude are expressed in kilometres.

Table A8 for details). Mean departure date from the natal area ranged from the 1 April for multi-rangers to the 14 May for progressive dispersers, while classic dispersers and aborted dispersers initiated dispersal, on average, the 20 April and the 2 May, respectively. However, there was also marked intra-class variation in departure date, especially for progressive dispersers (Supplementary material Appendix 3 Table A9). Finally, the straight line distance between the initial and final segment centroids also varied both between and within classes, ranging from 0.2 ± 0.1 km for strictly philopatric individuals to 12.9 ± 2.0 km for classic dispersers (±SD). In comparison to classic dispersers, aborted dispersers moved shorter distances from their natal range to their temporary settlement range (4.9 ± 2.6 km), while the distance between their natal and final settlement ranges (0.4 ± 0.1 km) was equivalent to that of strictly philopatric individuals. Progressive dispersers, multi-rangers and explorers moved the centroid of their range, on average, 1.0 ± 0.2, 0.7 ± 0.1 and 0.3 ± 0.03 km, respectively, between their initial and final ranges.

Drivers of alternative dispersal tactics

Based on the eigenvalues and PC scores (Supplementary material Appendix 4 Fig. A3, Table A10), for subsequent analyses we retained only the first axis of the PCA (PC1), explaining 85% of variation in landscape structure. Positive values of the PC1 indicated a low availability of crops and meadows in the home range, a low value of the Shannon index (low habitat heterogeneity) and a high distance to the nearest anthropogenic feature. PC1, thus, described a composite gradient of the availability of crops and meadows for feeding, landscape heterogeneity and disturbance.

1. Contrasting the environmental and phenotypic drivers of progressive dispersal versus classic dispersal

The set of retained models describing the propensity to adopt the progressive dispersal tactic rather than a classic dispersal tactic contained the PC1 of the landscape descriptors (all models within a ΔAICc of 2) and the two-way interaction between body mass and sex (Supplementary material Appendix 2 Table A3). The interaction indicated a negative relationship between the propensity to progressively disperse and body mass for females, but a positive one for males, however, these effects were weak (Table 1). In contrast, we found strong support for the hypothesis that the propensity to adopt a progressive dispersal rather than a classic dispersal tactic was linked to landscape structure in the natal range. The propensity to be a progressive disperser increased as the scores on the PC1 of landscape descriptors increased (estimate of 0.66 ± 0.31 (SE), n = 63 – Table 1), indicating that individuals living in the more homogeneous local landscapes, with lower resource quality, but subject to less anthropogenic disturbance, were more than twice as likely to adopt a progressive disperser tactic ($P_{\text{progressive disperser}} = 0.31$) than those living in the more heterogeneous open landscapes ($P_{\text{progressive disperser}} = 0.13$; Fig. 3a).

Table 1. Summary statistics from the model averaging procedure based on generalized linear models (within a ΔAICc of 2 from the best model), describing individual propensity to adopt a progressive dispersal tactic (versus a classic dispersal tactic) in relation to body mass, sex and landscape structure in the natal range. Landscape structure was indexed as the coordinates along the first axis of the PCA performed on three landscape descriptors (availability of crops and meadows, levels of habitat heterogeneity and anthropogenic disturbance in the natal range). We report parameter estimates (±SE) for each variable that featured in the retained models, z-values, confidence intervals at 2.5 and 97.5% (CI). The proportion of deviance explained by the model, calculated as the ratio between the residual (54.39) and null (66.74) deviances, was 0.815.

Variables	Estimates	SE	Z value	CI 2.5%	CI 97.5%
Intercept	1.34	4.93	0.27	−8.40	11.09
Landscape	0.66	0.31	2.08	0.04	1.29
Sex (male)	−1.32	6.15	0.21	−13.48	10.85
Body mass	−0.44	0.37	1.17	−1.18	0.30
Body mass × sex (male)	0.68	0.49	1.36	−0.30	1.65

2. Contrasting the environmental and phenotypic drivers of multi-ranging versus classic dispersal

The set of retained models describing the propensity of an individual to adopt the multi-range tactic rather than a classic dispersal tactic contained the PC1 of the landscape descriptors (almost all models within a ΔAICc of 2) and the two-way interaction between body mass and sex (Supplementary material Appendix 2 Table A4). The interaction indicated that the propensity to adopt the multi-range tactic increased as body mass decreased for males, but not for females (Table 2), but the effect was weak again. However, we found strong support for the hypothesis that the propensity of a juvenile roe deer to adopt a multi-range tactic rather than a classic dispersal tactic was linked to the landscape structure in its natal range. The propensity to adopt a multi-range tactic increased as the scores on the PC1 of landscape descriptors increased (estimate of 0.76 ± 0.36 (SE), n = 58 – Table 2), indicating that individuals living in the more homogeneous local landscapes, with lower resource quality, but subject to less anthropogenic disturbance, were more than nine times more likely to adopt a multi-range tactic ($P_{\text{multi-ranger}} = 0.28$) than those living in the more heterogeneous open landscapes ($P_{\text{multi-ranger}} = 0.03$; Fig. 3b).

3. Contrasting the environmental and phenotypic drivers of aborted dispersal versus classic dispersal

The set of retained models describing the propensity to abort the dispersal attempt (i.e. aborted dispersal versus classic dispersal) contained the additive effects of the PC1 of the landscape descriptors (all models within a ΔAICc of 2), body mass and sex (Supplementary material Appendix 2 Table A5). Once again, the influence of body mass and sex on the propensity to abort dispersal were only weakly supported (Table 3). In contrast, we found strong support for the hypothesis that the probability that a juvenile roe deer aborted its dispersal attempt was linked to landscape structure in the natal range. The propensity to abort a dispersal attempt increased as the

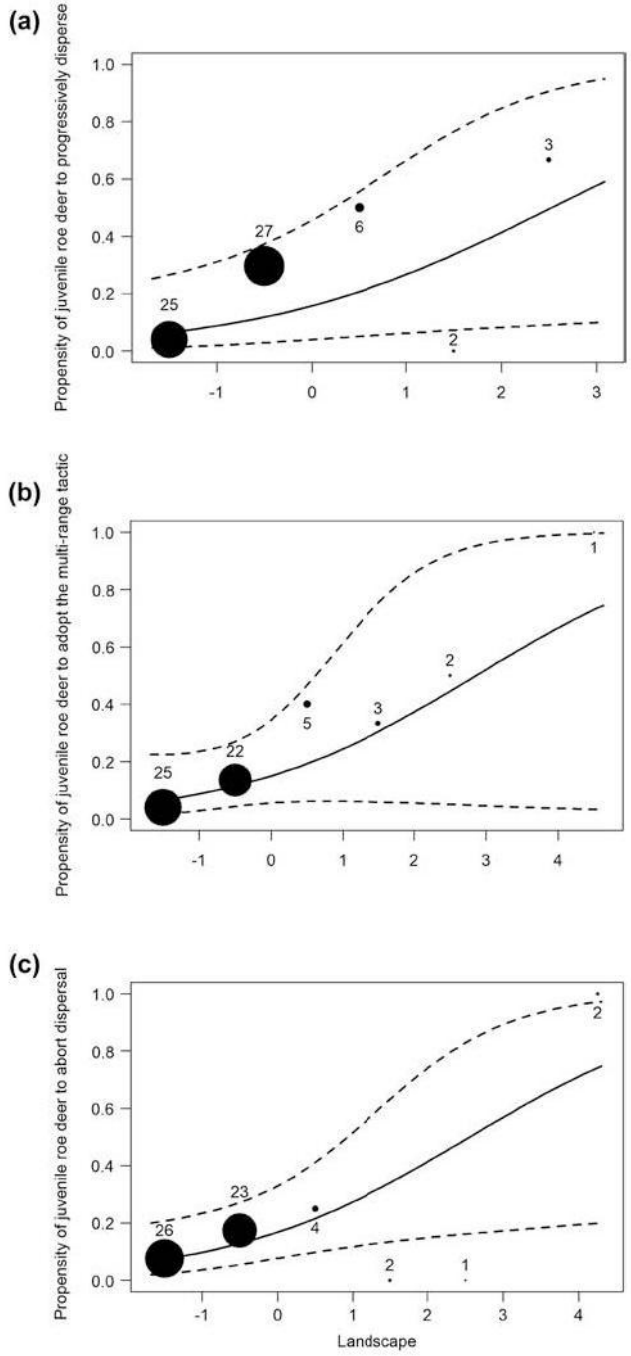


Figure 3. Variation in the propensity of juvenile roe deer to (a) progressively disperse, (b) adopt the multirange tactic, (c) abort their dispersal attempt (versus classically disperse) as a function of increasing landscape heterogeneity, availability of crops and meadows and anthropogenic disturbance (described by the PC1 of these three descriptors; low scores of the PC1 indicate a highly heterogeneous local landscape with both high levels of crops and meadows and high levels of anthropogenic disturbance). The line (and dotted lines) represents the model predictions (and the associated 95% confidence intervals). Points (proportional to sample size and centred for intervals of 1 unit of PC1) represent the observed propensity to adopt the given tactic for a given level of landscape heterogeneity, crop/meadow availability and disturbance.

Table 2. Summary statistics from the model averaging procedure based on generalized linear models (within a ΔAICc of 2 from the best model), describing individual propensity to adopt a multi-range tactic (versus a classic dispersal tactic) in relation to body mass, sex and landscape structure in the natal range. Landscape structure was indexed as the coordinates along the first axis of the PCA performed on three landscape descriptors (availability of crops and meadows, levels of habitat heterogeneity and anthropogenic disturbance in the natal range). We report parameter estimates (±SE) for each variable that featured in the retained models, z-values, confidence intervals at 2.5 and 97.5% (CI). The proportion of deviance explained by the model, calculated as the ratio between the residual (33.95) and null (50.06) deviances, was 0.678.

Variables	Estimates	SE	z-value	CI 2.5%	CI 97.5%
Intercept	−1.06	4.48	0.23	−10.01	7.89
Landscape	0.76	0.36	2.08	0.04	1.47
Body mass	−0.06	0.33	0.17	−0.71	0.60
Sex (male)	23.02	12.76	1.76	−2.56	48.60
Body mass × Sex (male)	−1.35	0.78	1.69	−2.91	0.22

scores on the PC1 of landscape descriptors increased (estimate of 0.62 ± (SE) 0.27, n = 58, DF = 2 – Table 3), such that individuals living in the more homogeneous landscapes, of poorer resource quality and with less anthropogenic disturbance in their natal range, were more than three times more likely to abort their dispersal attempt ($P_{\text{aborted disperser}} = 0.24$) than those living in the more heterogeneous open habitats ($P_{\text{aborted disperser}} = 0.07$; Fig. 3c).

Discussion

Marked heterogeneity among individuals in dispersal-related traits has been widely documented in recent times (Bowler and Benton 2005, Clobert et al. 2009), for example, in terms of propensity to disperse (Bonte et al. 2003) or distance travelled (Brown and Crone 2016). Here, using an exceptionally large and detailed data set on juvenile roe deer, we developed a novel methodology to identify six discrete

Table 3. Summary statistics from the model averaging procedure based on generalized linear models (within a ΔAIC_c of 2 from the best model), describing individual propensity to adopt an aborted dispersal tactic (versus a classic dispersal tactic) in relation to body mass, sex and landscape structure in the natal range. Landscape structure was indexed as the coordinates along the first axis of the PCA performed on three landscape descriptors (availability of crops and meadows, levels of habitat heterogeneity and anthropogenic disturbance in the natal range). We report parameter estimates (±SE) for each variable that featured in the retained models, z-values, confidence intervals at 2.5 and 97.5% (CI). The proportion of deviance explained by the model, calculated as the ratio between the residual (43.67) and null (50.06) deviances, was 0.872.

Variables	Estimates	SE	z-value	CI 2.5%	CI 97.5%
Intercept	−2.06	2.14	0.94	−6.33	2.22
Landscape	0.62	0.27	2.23	0.08	1.17
Sex (male)	0.70	0.82	0.83	−0.95	2.34
Body mass	0.13	0.25	0.52	−0.37	0.63

alternative behavioural tactics during dispersal. These tactics were characterised by different timing, amplitude and directionality in movement behaviour. A post hoc analysis based on movement parameters revealing inter- and intra-individual variation in movement behaviour (Supplementary material Appendix 5) indicated that our classification was moderately robust, allowing us to classify individuals into ecologically meaningful groups and suggesting that our methodology could be informative for other study systems. We also demonstrated that the expression of these alternative tactics was over-ridingly influenced by the individual's natal environment. Our work indicates that individuals may adopt a variety of alternative movement tactics during natal dispersal in response to particular proximal drivers, with potentially important impacts for population dynamics (Clobert et al. 2009).

Natal dispersal promotes gene flow and influences population structure, in particular, by determining the geographical distance between close relatives and, thereby, limiting inbreeding (Bohonak 1999). Because roe deer adults have very high site fidelity to their post-dispersal range (Linnell and Andersen 1998), with about 93.5% of individuals remaining faithful to their settlement range (Material and methods, Supplementary material Appendix 1), they most likely reproduce where they settle at the end of dispersal transience. The six alternative dispersal tactics that we identified are, hence, likely to have contrasting implications for gene flow and population structure. Classic dispersers should contribute most to gene flow as they dispersed, on average, more than 10 kilometres (equivalent to around 10 home range diameters), well beyond any spatial structure in relatedness (Bonnot et al. 2010). In contrast, the role of aborted dispersal for gene flow may differ between the sexes, because females (Hewison 1996), but not males (Vanpé et al. 2009), are sexually active at 15 months of age in roe deer. Therefore, although all but two (both males) of the nine aborted dispersers spent at least part of that summer rut on their aborted dispersal range prior to returning to their natal range (mean aborted dispersal duration = 84.8 ± 59.6 days (SD)), only the five females actually likely copulated there. This behaviour would appear to be the reproductive equivalent of the rut excursion behaviour that has been widely reported in female roe deer adults (Debeffe et al. 2014), generating female-mediated gene flow of the male genome over intermediate distances, contrary to classic dispersal, which generates gene flow of both male and female genomes. In contrast, progressive dispersal and multi-ranging tactics result in settlement in an immediately neighbouring range, with little potential impact on gene flow at the landscape scale, but likely facilitating avoidance of incestuous mating with parents.

Phenotype-dependence in the propensity of an individual to disperse is widespread across organisms (Clobert et al. 2009). For example, heavier individuals have been shown to disperse more often and further compared to lighter individuals in a variety of species (Barbraud et al. 2003, Searcy et al. 2018), including roe deer (Debeffe et al. 2012). Heavier individuals are likely better able to offset the costs of dispersal (Bonte et al. 2012) and may be able to settle more easily in a novel range (Stamps 2006). Our results support previous work showing that heavy individuals have a greater propensity to disperse long distances (i.e. 'classic dispersal' in our study, results not shown; see Debeffe et al. 2012), but indicate that body condition is not a determinant of whether an individual successfully settles or, rather, aborts its dispersal attempt. Furthermore, there was only a weak evidence for sex-specific influence of body mass on the propensity of an individual to use the multi-range or progressive dispersal tactics. Thus, because these two alternative tactics require no real increase in overall mobility compared to philopatry, we suggest that the role of body mass in determining dispersal tactics is likely related to the capacity of an individual to offset the associated costs of dispersal in relation to its sex. Our results might also suggest that the ultimate drivers of dispersal tactics are sex-specific, as classic dispersal was slightly female-biased (61.2% female), while slightly more males were progressive dispersers or multi-rangers (60.9% male). Because this contrasts with previous findings (Coulon et al. 2006, Gaillard et al. 2008), additional data will be required to explore whether dispersal tactics do really differ between the sexes.

If dispersal is a response to density-dependent scramble competition for resources (Bowler and Benton 2005, Clobert et al. 2012), individuals should base their dispersal decisions on the quality of their natal habitat (Stamps 2006) relative to the surrounding alternative habitat (Matthysen 2012). Here, we demonstrated that dispersing individuals that were born on a higher quality and heterogeneous natal range almost exclusively adopted a classic dispersal tactic, whereas around half of all dispersers that were born in lower quality homogeneous forest habitat adopted either a progressive dispersal tactic (Fig. 3a) or a multi-range tactic (Fig. 3b). There are at least two non-mutually exclusive interpretations of these results. First, high availability of crops and meadows in the natal range promotes rapid growth so that juveniles born in the most open sectors of the landscape are around 20% heavier than those in pure forest habitat (Hewison et al. 2009). Hence, these individuals may be better able to offset the costs of classic long-range dispersal (Bonte et al. 2012) compared to individuals living in poorer habitat which may be forced to adopt the alternative, short-range, and presumably less costly, movement tactics. Alternatively, juveniles born in the open agricultural landscapes are likely habituated to a high level of habitat patchiness and baseline anthropogenic disturbance. As a consequence, they may be less reluctant to cross habitat boundaries (Wiens 1976) and better able to deal with the alien landscape of fear through which they must navigate during classic dispersal transience and settlement. This interpretation is supported by the observation that individuals which subsequently aborted their dispersal attempt were also predominantly born in the more homogeneous and less disturbed forest habitats (Fig. 3c, Supplementary material

Appendix 4 Table A11). Detailed comparison of the habitat characteristics of natal and settlement ranges should provide a better understanding of why around 15% of dispersers abandon their settlement range after only a few months residence and return to their natal site.

Our work provides further evidence of the huge complexity in dispersal behaviour. Within the theoretical framework developed by Baguette and Fagan (2014), it seems likely that the alternative dispersal tactics we identified are responses to different selective pressures. For example, short dispersal distances may suffice to avoid kin competition and inbreeding (Baguette and Fagan 2014), in particular between parents and offspring, which might generate a progressive dispersal or multi-range tactic linked to the spatial structure of relatedness. In contrast, density-dependent conspecific competition for resources is likely to select for long distance dispersal (i.e. 'classic dispersal'), notably in response to environmental heterogeneity, driving emigration from the population (Baguette and Fagan 2014). The next step will be to quantify the link between dispersal behaviour and individual performance so as to better understand the ultimate drivers of different dispersal tactics and their consequences for gene flow and population structure.

Acknowledgments – We would like to thank all the CEFS, ONCFS staff and all the field volunteers who participated in roe deer captures. We thank the local hunting associations and the Fédération Départementale des Chasseurs de la Haute Garonne for allowing us to work in the study area. We also would like to thank Jeffrey Carbillet, Laura Gervais and Ophélie Couriot for their insightful comments and constructive discussions.

Funding – This project (DISPCOST) was funded by the Agence Nationale de la Recherche (ANR), grant no. ANR-15-CE02-0008 obtained by AC.

Conflicts of interest – The authors declare that they have no conflict of interest.

Authors contributions – A. Coulon and A. J. M. Hewison contributed equally to this paper. AC, AJMH and NM conceived the original idea for this manuscript; DD, AC, AJMH, NM, LD, BC, BL and YC participated in data collection; DD, AC, AJMH and NM designed the methodology and analysed the data; RP and KA assisted with the analytical approach; DD, AC, AJMH and NM led the writing of the manuscript, with inputs from all contributing authors. All authors gave final approval for publication.

Permits – All capture and marking procedures were done in accordance with French and European laws for animal welfare (prefectural order from the Toulouse Administrative Authority to capture and monitor wild roe deer and agreement no. A31113001 approved by the Departmental Authority of Population Protection).

References

Adrados, C. et al. 2003. GPS approach to study fine-scale site use by wild red deer during active and inactive behaviors. – Wildl. Soc. Bull. 31: 544–552.

Baguette, M. et al. 2014. The pros and cons of applying the movement ecology paradigm for studying animal dispersal. – Mov. Ecol. 2: 1–13.

Barbraud, C. et al. 2003. Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. – J. Anim. Ecol. 72: 246–257.

Barraquand, F. and Benhamou, S. 2008. Animal movements in heterogeneous landscapes: identifying profitable places and homogeneous movement bouts. – Ecology 89: 3336–3348.

Barton, K. 2018. MuMIn: multi-model inference. – R package ver. 1.40.4.

Bivand, R. and Rundel, C. 2017. rgeos: interface to geometry engine – Open Source ('GEOS'). R package ver. 0.3-26. <https://CRAN.R-project.org/package=rgeos>.

Bohonak, A. J. 1999. Dispersal, gene flow and population structure. – Q. Rev. Biol. 74: 21–45.

Bonnot, N. et al. 2010. No difference between the sexes in fine-scale spatial genetic structure of roe deer. – PLoS One 5: e14436.

Bonte, D. et al. 2003. Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. – Proc. R. Soc. B 270: 1601–1607.

Bonte, D. et al. 2006. Aerial dispersal plasticity under different wind velocities in a salt marsh wolf spider. – Behav. Ecol. 18: 438–443.

Bonte, D. et al. 2008. Thermal conditions during juvenile development affect adult dispersal in a spider. – Proc. Natl Acad. Sci. USA 105: 17000–17005.

Bonte, D. et al. 2012. Costs of dispersal. – Biol. Rev. 87: 290–312.

Börger, L. et al. 2006. Effects of sampling regime on the mean and variance of home range size estimates. – J. Anim. Ecol. 75: 1393–1405.

Bougeard, S. and Dray, S. 2018. Supervised multiblock analysis in R with the ade4 Package. – J. Stat. Softw. 86: 1–17.

Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – Biol. Rev. 80: 205–225.

Bracis, C. et al. 2018. Revisitation analysis uncovers spatio-temporal patterns in animal movement data. – Ecography 41: 1801–1811.

Braendle, C. et al. 2006. Wing dimorphism in aphids. – Heredity 97: 192–199.

Breiman, L. 2001. Random forests. – Mach. Learn. 45: 5–32.

Brown, L. M. and Crone, E. E. 2016. Individual variation changes dispersal distance and area requirements of a checkerspot butterfly. – Ecology 97: 106–115.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. – Springer.

Calenge, C. 2006. The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. – Ecol. Model. 197: 516–519.

Clobert, J. et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. – Ecol. Lett. 12: 197–209.

Clobert, J. et al. 2012. Dispersal ecology and evolution. – Oxford Univ. Press.

Coulon, A. et al. 2004. Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual–based approach. – Mol. Ecol. 13: 2841–2850.

Coulon, A. et al. 2006. Dispersal is not female biased in a resource-defence mating ungulate, the European roe deer. – Proc. R. Soc. B 273: 341–348.

Couriot, O. et al. 2018. Truly sedentary? The multi-range tactic as a response to resource heterogeneity and unpredictability in a large herbivore. – Oecologia 187: 47–60.

Debeffe, L. et al. 2012. Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. – J. Anim. Ecol. 81: 1327–1327.
Debeffe, L. et al. 2013. Exploration as a key component of natal dispersal: dispersers explore more than philopatric individuals in roe deer. – Anim. Behav. 86: 143–151.
Debeffe, L. et al. 2014. A one night stand? Reproductive excursions of female roe deer as a breeding dispersal tactic. – Oecologia 176: 431–443.
Doerr, E. D. and Doerr, V. A. 2005. Dispersal range analysis: quantifying individual variation in dispersal behaviour. – Oecologia 142: 1–10.
Ducros, D. et al. 2019. Data from: Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.3s41j61>.
Elliot, N. B. et al. 2014. Movements vary according to dispersal stage, group size and rainfall: the case of the African lion. – Ecology 95: 2860–2869.
Environmental Systems Research Institute (ESRI) 2018. ArcGIS release 10.6.1. Redlands, CA.
Fey, K. et al. 2016. Roads are no barrier for dispersing red squirrels in an urban environment. – Behav. Ecol. 27: 741–747.
Fronhofer, E. A. et al. 2018. Bottom-up and top-down control of dispersal across major organismal groups. – Nat. Ecol. Evol. 2: 1859–1863.
Gaillard, J. M. et al. 2008. Population density and sex do not influence fine-scale natal dispersal in roe deer. – Proc. R. Soc. B 275: 2025–2030.
Gibbs, M. et al. 2010. Organisms on the move: ecology and evolution of dispersal. – Biol. Lett. 6: 146–148.
Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. – Anim. Behav. 28: 1140–1162.
Haughland, D. L. and Larsen, K. W. 2004. Exploration correlates with settlement: red squirrel dispersal in contrasting habitats. – J. Anim. Ecol. 73: 1024–1034.
Hewison, A. J. M. 1996. Variation in the fecundity of roe deer in Britain: effects of age and body weight. – Acta Theriol. 41: 187–198.
Hewison, A. J. M. et al. 1998. Social organisation of European roe deer. – In: Andersen, R. et al. (eds), The European roe deer: the biology of success. Scandinavian Univ. Press, Oslo, pp. 189–219.
Hewison, A. M. et al. 2007. Using radio-tracking and direct observation to estimate roe deer *Capreolus capreolus* density in a fragmented landscape: a pilot study. – Wildl. Biol. 13: 313–320.
Hewison, A. J. et al. 2009. Landscape fragmentation influences winter body mass of roe deer. – Ecography 32: 1062–1070.
Hogan, J. D. et al. 2014. Consequences of alternative dispersal strategies in a putatively amphidromous fish. – Ecology 95: 2397–2408.
Holyoak, M. et al. 2008. Trends and missing parts in the study of movement ecology. – Proc. Natl Acad. Sci. USA 105: 19060–19065.
Jacob, S. et al. 2016. Cooperation-mediated plasticity in dispersal and colonization. – Evolution 70: 2336–2345.
Kays, R. et al. 2015. Terrestrial animal tracking as an eye on life and planet. – Science 348: aaa2478.
Kenward, R. E. et al. 2002. From marking to modelling: dispersal study techniques for land vertebrates. – In: Bullock, J. M. et al. (eds), Dispersal ecology. Blackwell, pp. 50–71.
Lavielle, M. 1999. Detection of multiple changes in a sequence of dependent variables. – Stoch. Process. Their. Appl. 83:79–102.
Linnell, J. D. and Andersen, R. 1998. Territorial fidelity and tenure in roe deer bucks. – Acta Theriol. 43: 67–75.
Maag, N. et al. 2019. Cost of dispersal in a social mammal: body mass loss and increased stress. –Proc. R. Soc. B 286: 20190033.
Martin, J. et al. 2018. Temporal shifts in landscape connectivity for an ecosystem engineer, the roe deer, across a multiple-use landscape. – Landscape Ecol. 33: 937–954.
Martorell, C. and Martínez-López, M. 2014. Informed dispersal in plants: *Heterosperma pinnatum* (Asteraceae) adjusts its dispersal mode to escape from competition and water stress. – Oikos 123: 225–231.
Matthysen, E. 2012. Multicausality of dispersal: a review. – In: Clobert, J. et al. (eds), Dispersal ecology and evolution. – Oxford Univ. Press, pp. 3–18.
Mayer, M. et al. 2017. When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. – Anim. Behav. 123: 375–382.
Morellet, N. et al. 2009. The effect of capture on ranging behaviour and activity of the European roe deer *Capreolus capreolus*. – Wildl. Biol. 15: 278–287.
Morellet, N. et al. 2011. Landscape composition influences roe deer habitat selection at both home range and landscape scales. – Landscape Ecol. 26: 999–1010.
Morellet, N. et al. 2013. Seasonality, weather and climate affect home range size in roe deer across a wide latitudinal gradient within Europe. – J. Anim. Ecol. 82: 1326–1339.
Mucherino, A. et al. 2009. K-nearest neighbor classification. – In: Data mining in agriculture. Springer, pp. 83–106.
Patin, R. et al. 2018. Identifying stationary phases in multivariate time-series for highlighting behavioural modes and home range settlements. – J. Anim. Ecol. in press.
Ratcliffe, P. R. and Mayle, B. A. 1992. Roe deer biology and management. – HMSO, London.
Rémy, A. et al. 2011. Effects of individual condition and habitat quality on natal dispersal behaviour in a small rodent. – J. Anim. Ecol. 80: 929–937.
Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. – Annu. Rev. Ecol. Evol. Syst. 38: 231–253.
Ronce, O. and Clobert, J. 2012. Dispersal syndromes. – In: Clobert, J. et al. (eds), Dispersal ecology and evolution. – Oxford Univ. Press pp. 119–138.
Searcy, C. A. et al. 2018. Positive correlation between dispersal and body size in green frogs (*Rana clamitans*) naturally colonizing an experimental landscape. – Can. J. Zool. 96: 1378–1384.
Stamps, J. A. 2006. The silver spoon effect and habitat selection by natal dispersers. – Ecol. Lett. 9: 1179–1185.
Stamps, J. A. et al. 2005. Search costs and habitat selection by dispersers. – Ecology 86: 510–518.
Torrents-Ticó, M. et al. 2018. Growth affects dispersal success in social mole-rats, but not the duration of philopatry. – Biol. Lett. 14: 20180005.
VanderWaal, K. L. et al. 2009. Optimal group size, dispersal decisions and postdispersal relationships in female African lions. – Anim. Behav. 77: 949–954.
Van Moorter, B. et al. 2008. Evidence for exploration behaviour in young roe deer (*Capreolus capreolus*) prior to dispersal. – Ethol. Ecol. Evol. 20: 1–15.

Vanpé, C. et al. 2009. Age-specific variation in male breeding success of a territorial ungulate species, the European roe deer. – J. Mammal. 90: 661–665.
Vanpé, C. et al. 2016. Immune gene variability influences roe deer natal dispersal. – Oikos 125: 1790–1801.
Venables, W. N. and Ripley, B. D. 2002. Modern applied statistics with S. 4th edn. – Springer ISBN 0-387-95457-0.

Supplementary material (available online as Appendix oik-06793 at <www.oikosjournal.org/appendix/oik-06793>). Appendix 1–5.

Wahlström, L. K. and Liberg, O. 1995. Patterns of dispersal and seasonal migration in roe deer (*Capreolus capreolus*). – J. Zool. 235: 455–467.
Wiens, J. A. 1976. Population responses to patchy environments. – Annu. Rev. Ecol. Syst. 7: 81–120.
Worton, B. J. 1989. Kernel methods for estimating the utilization distribution. – Ecology 70: 164–168.

Supplementary Materials

Appendix I: Spatial fidelity in roe deer

To estimate spatial fidelity in our study population, we quantified the degree of overlap in locations of those individuals for which we had spatial information that covered several years. For individuals that were VHF- or GPS- monitored over at least two years during their lifetime, we measured range overlap using 50% fixed kernels between the post-dispersal range and the adult range, or between two subsequent adult ranges (see Tables S1 and S2) (libraries 'adehabitatHR', Calenge 2006 and 'rgeos', Bivand and Rundel 2017). In addition, for those that were monitored only one year, but were subsequently recovered when they died, we compared their location at death to the locations during the monitoring period, using graphs ('plot' function in R) (see Figure A1). When location at death or the adult range overlapped with the post-settlement range or the adult range in a previous year, we considered the animal to be faithful to its home range.

Firstly, of the 58 adults that were monitored during two or more years, 54 (~ 93 %) were faithful to their core home range. Second, of the 30 juveniles that were monitored by GPS during the post-dispersal phase, 28 (~ 93%) were subsequently located within their settlement range during adulthood.

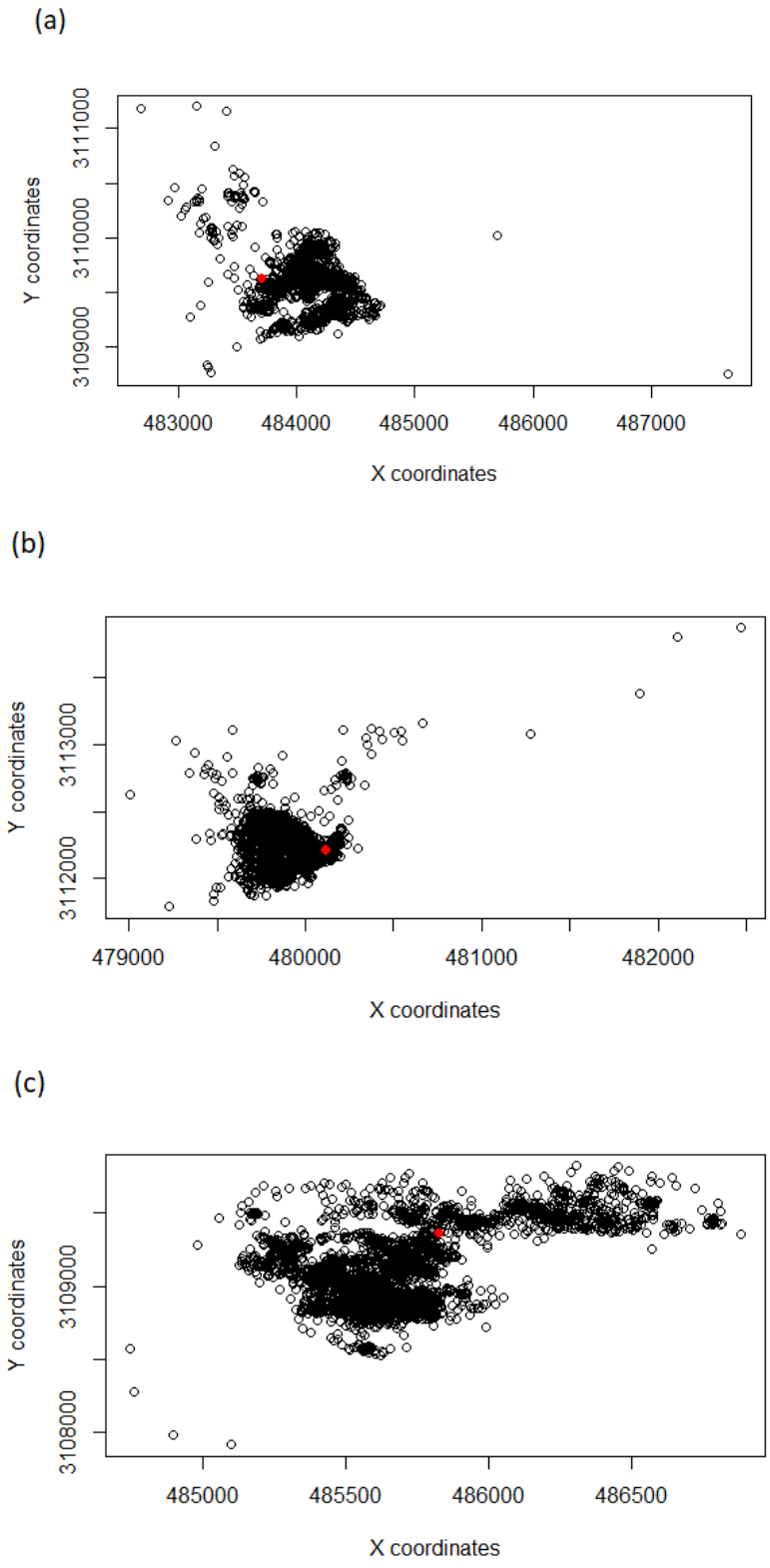
Table A1 : Overlap between the post-dispersal range and the adult range for 15 individuals monitored both as a juvenile and an adult – Overlap was measured using a 50 % kernel – ID : individual identity ; a value of 0 indicates the ranges did not overlap

ID	Overlap (%)
378	76.97
412	0
444	80.25
486	31.35
504	73.28
516	85.52
722	59.11
738	99.04
858	79.67
900	7.021
931	35.75
955	66.32
984	30.38
F1213	0.4541
F1347	75.17

Table A2 : Overlap between successive adult annual ranges for GPS-tracked adult roe deer – Overlap was measured using a 50 % kernel – ID : individual identity ; a value of 0 indicates the ranges did not overlap

ID	Overlap (%)
252	99
260	0
426	44.54
328	63.04
504	54.76
746	66.56
806	70.96
820	89.86
542	69.27
818	69.41
F572	84.43
104	0
202	77.31
212	46.06
390	92.23
484	0
572	99.92
672	90.9
7	81.15
778	92.26
838	75.01
916	51.68
932	92.07
968	0
47	84.83

Figure A1: Examples of overlap between the location at death and locations from GPS devices for three individuals (a, b and c). Individual 'a' died five years after the monitoring period, and individuals 'b' and 'c' died two years after the monitoring period. The location at death is represented by a red point on each figure. All locations at death were clearly within the previous home range.



Reference for this Appendix I

Bivand, R. and Rundel, C. 2017. rgeos: Interface to Geometry Engine - Open Source ('GEOS'). R package version 0.3-26. https://CRAN.R-project.org/package=rgeos

Calenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. – Ecol. Model. 197: 516–519.

Appendix II: Generalised Linear Models and Multinomial Models to investigate drivers of alternative dispersal tactics

Table A3: Candidate generalised linear models in a deltaAICc of 2 describing individual propensity to adopt a progressive dispersal tactic (vs. a classic dispersal tactic) in relation to body mass, sex and landscape structure. We also report the results for the null model. The landscape variable was calculated as the coordinates along the first axis of the PCA performed on the landscape descriptors (availability of crops and meadows, levels of landscape heterogeneity and anthropogenic disturbance). The reference class is classic dispersal and the reference sex is female. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc), the number of estimated parameters (df), AICc weights, null and residual deviances, as well as the percentage of deviance explained (ratio).

Model	df	AICc	detaAICc	AICc Weight	Null deviance	Residual deviance	Ratio
Landscape + sex	3	64.1	0.0	0.35	66.74	57.73	86.50
Landscape	2	65.0	0.9	0.23		60.78	91.07
Landscape + body mass + sex	4	65.2	1.1	0.20		56.48	84.63
Landscape + body mass*sex	5	65.4	1.3	0.18		54.39	81.50
Null model	1	68.8	4.7	0.03		66.74	100

Table A4: Candidate generalised linear models in a deltaAICc of 2 describing individual propensity to adopt a multi-range tactic (vs. a classic dispersal tactic) in relation to body mass, sex and landscape structure. We also report the results for the null model. The landscape variable was calculated as the coordinates along the first axis of the PCA performed on the landscape descriptors (availability of crops and meadows, levels of landscape heterogeneity and anthropogenic disturbance). The reference class is classic dispersal and the reference sex is female. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df), AICc weights, null and residual deviances, as well as the percentage of deviance explained (ratio).

Model	df	AICc	detaAICc	AICc Weight	Null deviance	Residual deviance	Ratio
Landscape + body mass*sex	5	45.1	0.0	0.33	50.06	33.95	67.82
Landscape	2	45.4	0.3	0.23		41.14	82.18
Body mass*sex	4	46.1	1.0	0.20		37.39	74.69
Landscape + body mass	3	46.5	1.4	0.17		40.03	79.96
Null model	1	52.1	7.0	0.01		50.06	100

Table A5: Candidate generalised linear models in a deltaAICc of 2 describing individual propensity to adopt an aborted dispersal tactic (vs. a classic dispersal tactic) in relation to body mass, sex and landscape structure. We also report the results for the null model. The landscape variable was calculated as the coordinates along the first axis of the PCA performed on the landscape descriptors (availability of crops and meadows, levels of landscape heterogeneity and anthropogenic disturbance). The reference class is classic dispersal and the reference sex is female. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df), AICc weights, null and residual deviances, as well as the percentage of deviance explained (ratio).

Model	df	AICc	detaAICc	AICc Weight	Null deviance	Residual deviance	Ratio
Landscape	2	48.6	0.0	0.50	50.06	44.41	88.71
Landscape + sex	3	50.1	1.5	0.24		43.69	87.28
Landscape + body mass	3	50.6	2.0	0.1		44.13	88.15
Null model	1	52.1	3.5	0.09		50.06	100

Table A6: Candidate multinomial models describing individual propensity to adopt one of the four alternative tactics (vs. a classic dispersal tactic) in relation to body mass, sex and landscape structure within a deltaAICc of 10. We also report the results for the null model. Philopatric individuals were combined with explorers. The landscape variable was calculated as the coordinates along the first axis of the PCA performed on the landscape descriptors (availability of crops and meadows, levels of landscape heterogeneity and anthropogenic disturbance). The reference class is classic dispersal and the reference sex is female. Models are ranked by order of increasing AICc; we report the ΔAICc (difference in AICc values between a given model and the model with the lowest AICc) and the number of estimated parameters (df).

Model	df	AICc	deltaAICc
Landscape	8	374.69	0.0
Landscape + sex	12	380.44	5.7
Landscape + body mass	12	382.13	7.4
Null model	4	386.43	11.7

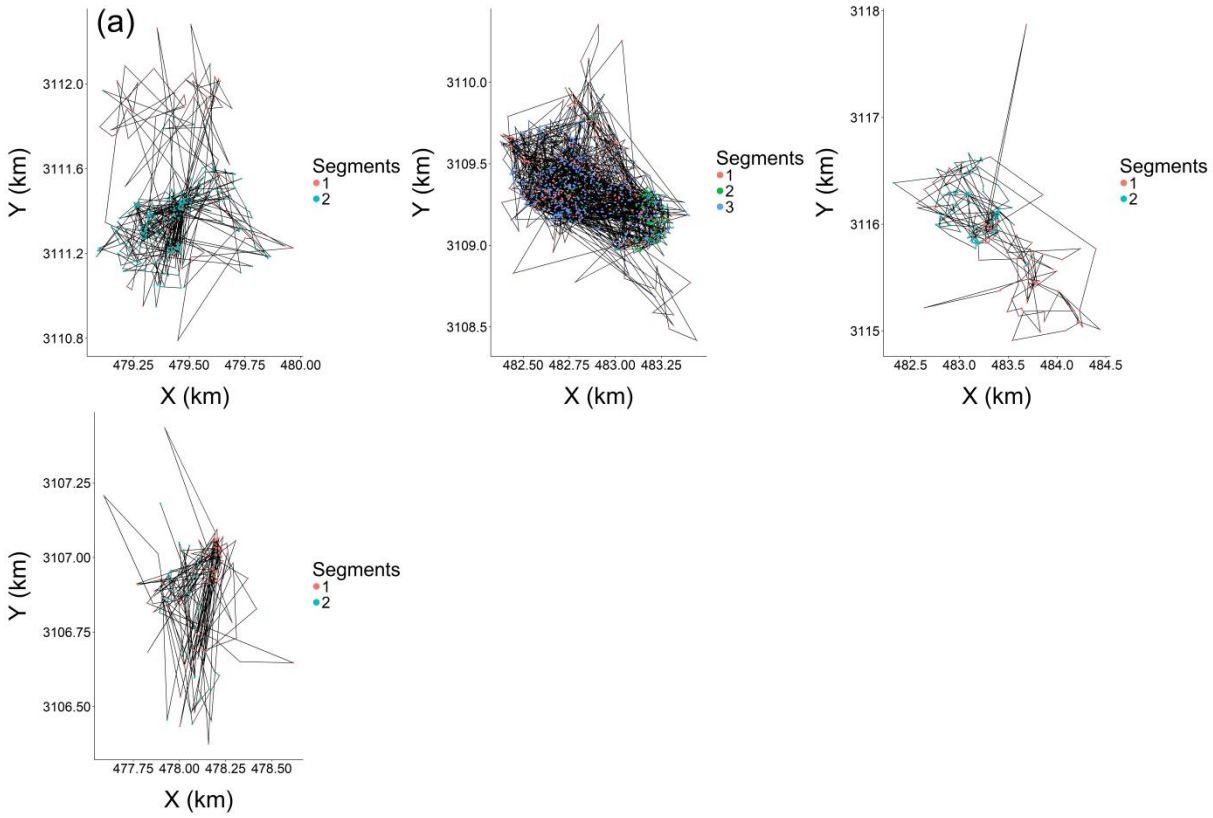
Table A7: Summary statistics from the model averaging procedure based on multinomial models discriminating all dispersal tactics (classic dispersers, aborting dispersers, progressive dispersers, multi-rangers and philopatric individuals, i.e. a combination of strict philopatric individuals and explorers) based on landscape, sex and body mass – classic dispersers constitute the reference class and the reference sex is female. Models were run using the function multinom from the library ('mgcv' – Wood 2011). We report estimates, standard errors, null and residual deviances, as well as the pourcentage of deviance explained (Ratio).

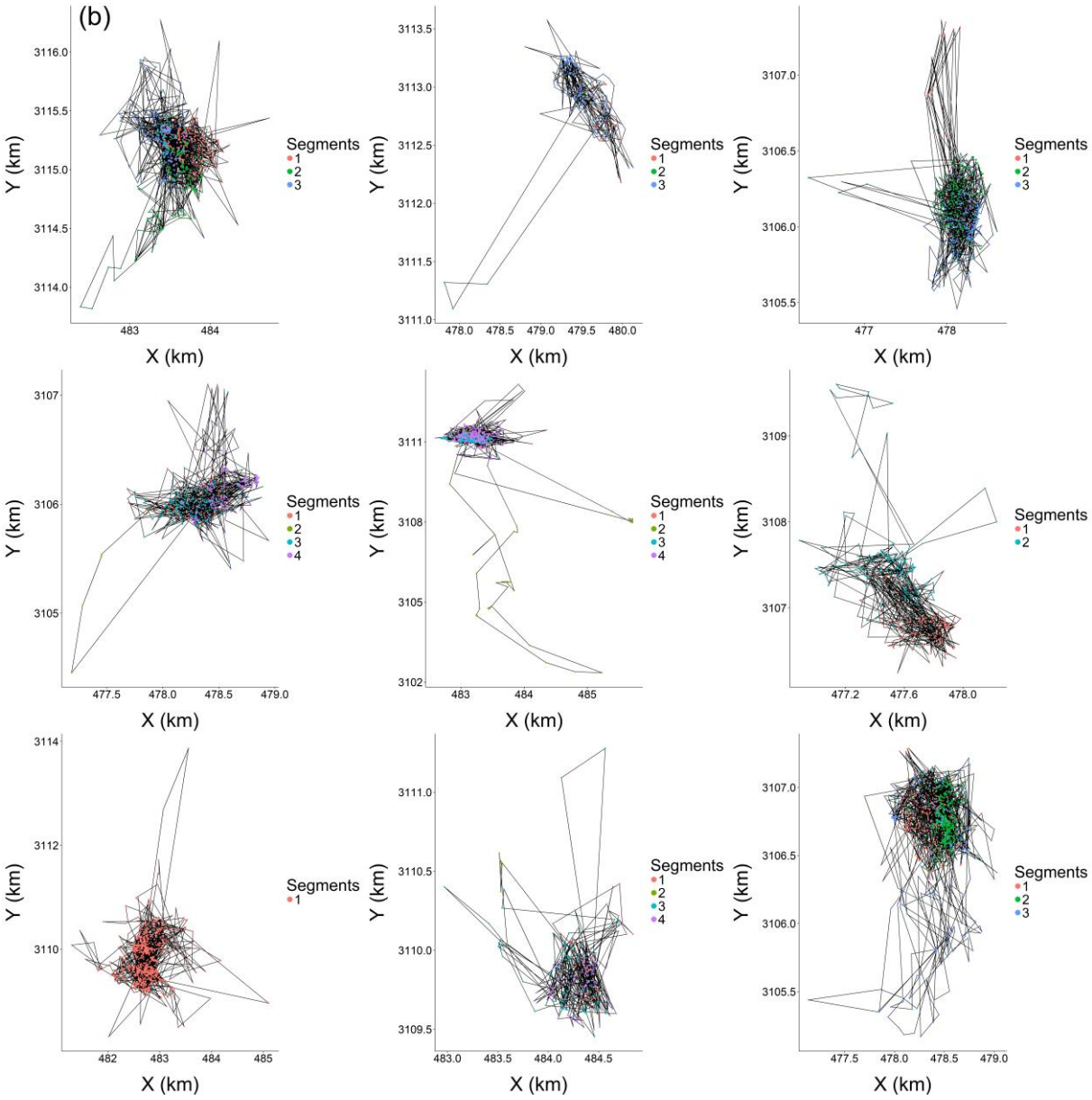
	Coefficients				**Null deviance**	**Residual deviance**	**Ratio**
	Intercept	SE (intercept)	Landscape	SE (Landscape)	378.15	357.65	94.58
Progressive dispersers	-1.00	0.33	0.62	0.26			
Multi-rangers	-1.52	0.41	0.82	0.27			
Philopatric individuals	0.52	0.24	0.71	0.22			
Aborted dispersers	-1.47	0.40	0.75	0.27			

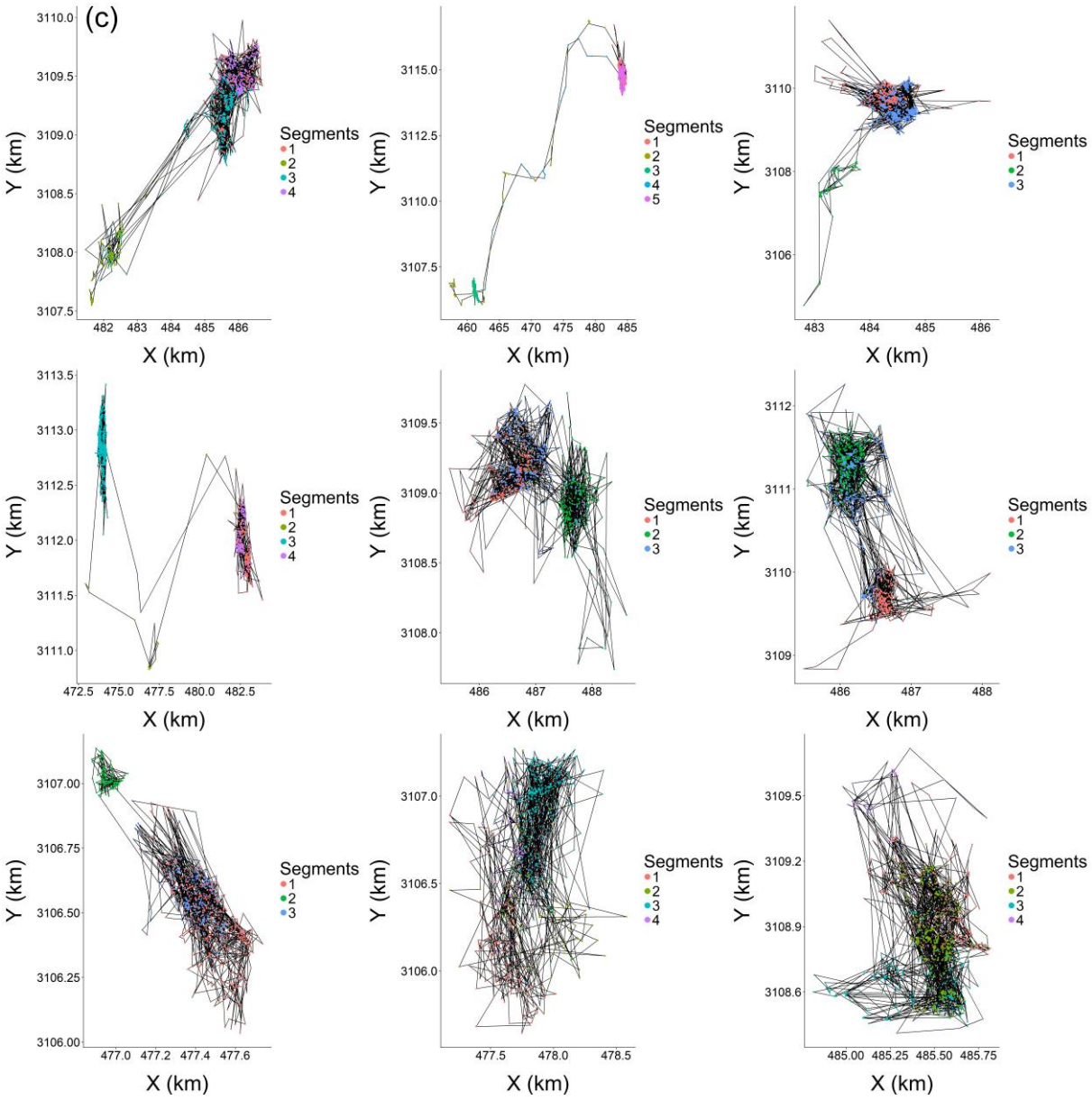
Reference for this appendix II

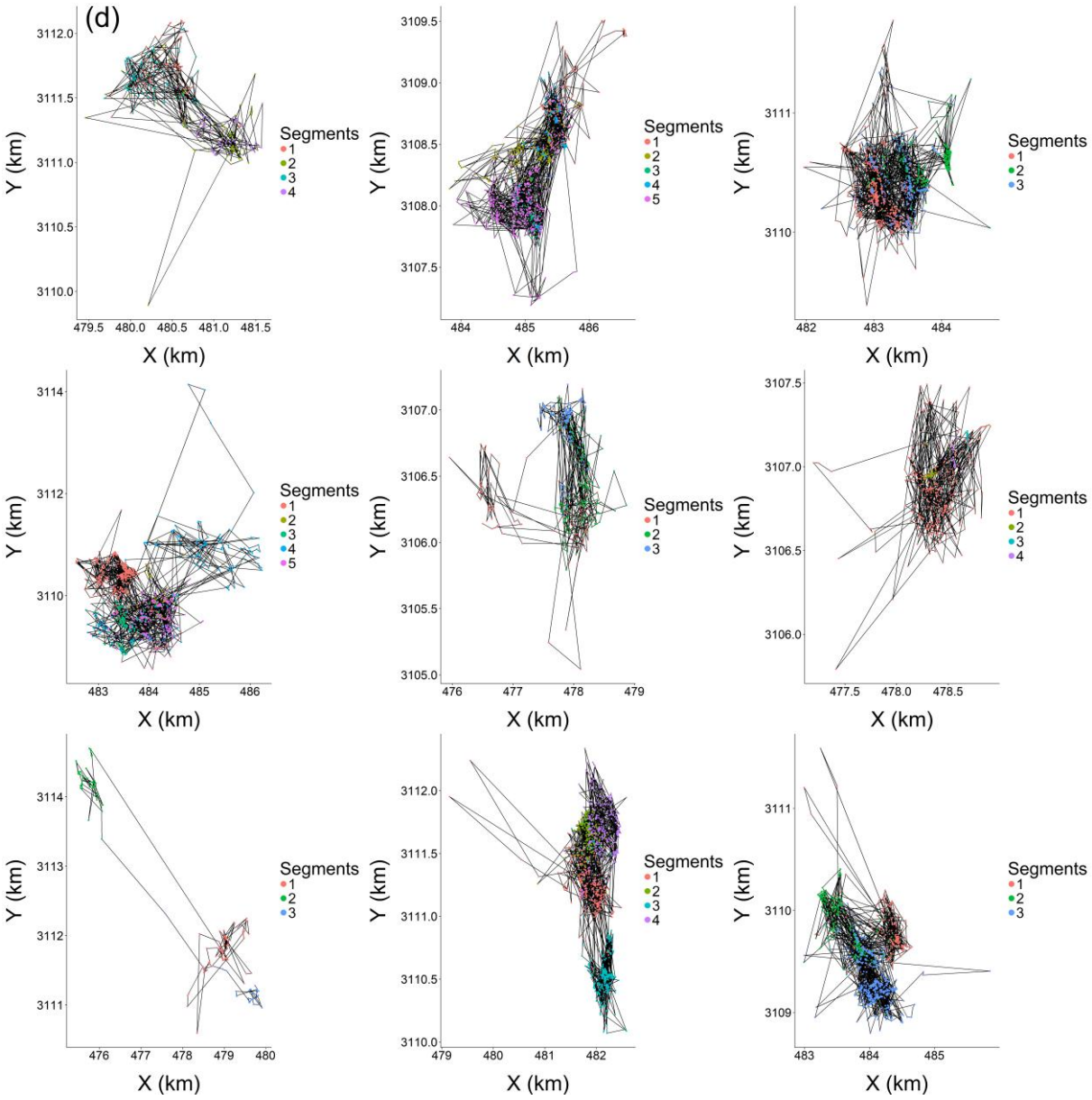
Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. – Journal of the Royal Statistical Society (B) 73:3–36

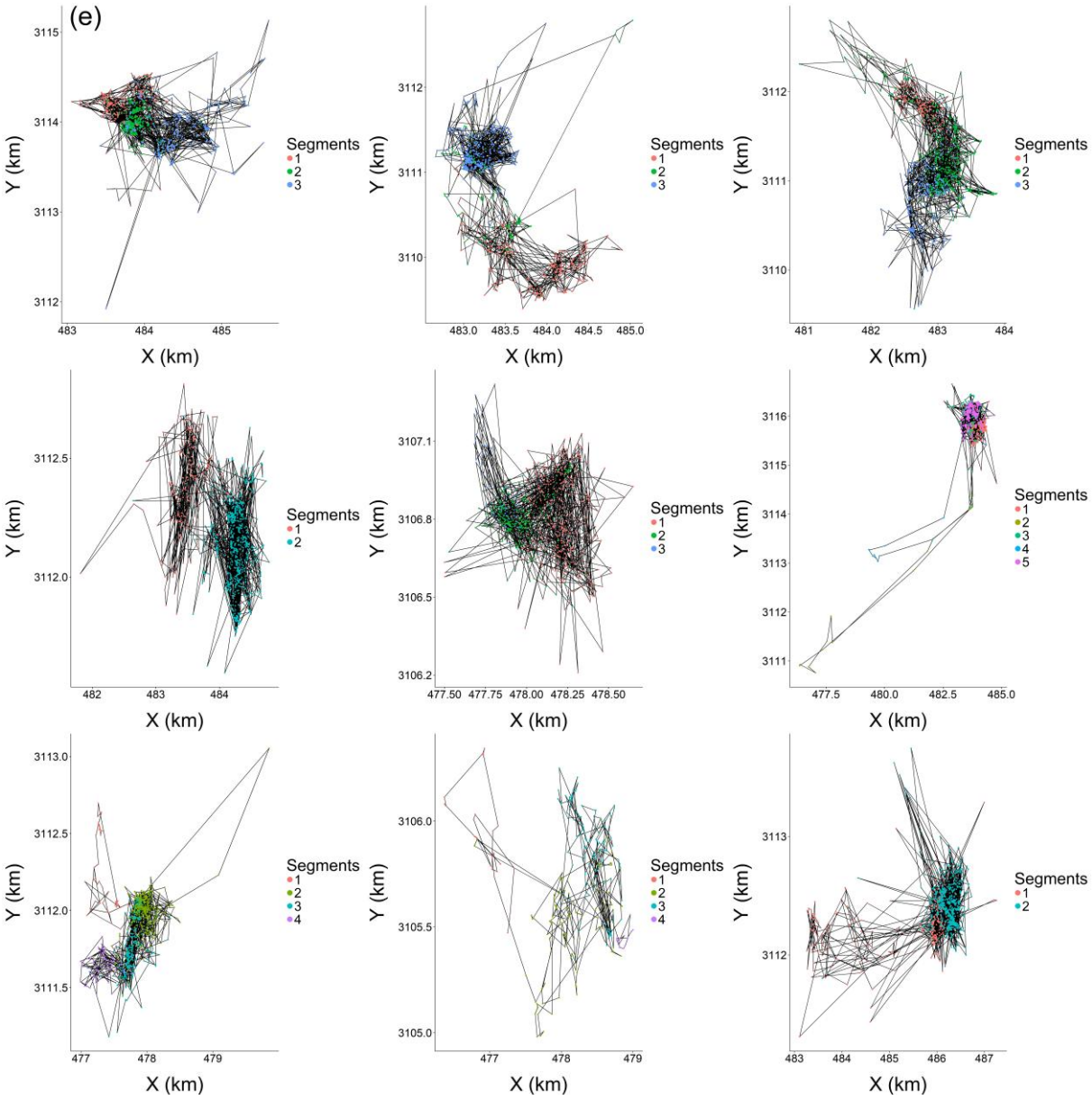
Figure A2: Additional examples of individual trajectories for each movement tactic exhibited by roe deer, as assigned by our classification: a. Strict philopatric; b. Explorer; c. Aborted disperser; d. Multi-ranger; e. Progressive disperser; f. Classic disperser. Each dot represents a GPS location, and successive locations are linked by a straight line. Successive segments identified by the segmentation approach are coded in different colours and numbered chronologically. X and Y coordinates are expressed in kilometres.




(b)
Y (km)
X (km)
Segments
1
2
3
4


(c)
Y (km)
X (km)
Segments
1
2
3
4
5


(d)
Y (km)
X (km)
Segments
1
2
3
4
5


(e)
Y (km)
X (km)
Segments
1
2
3
4
5

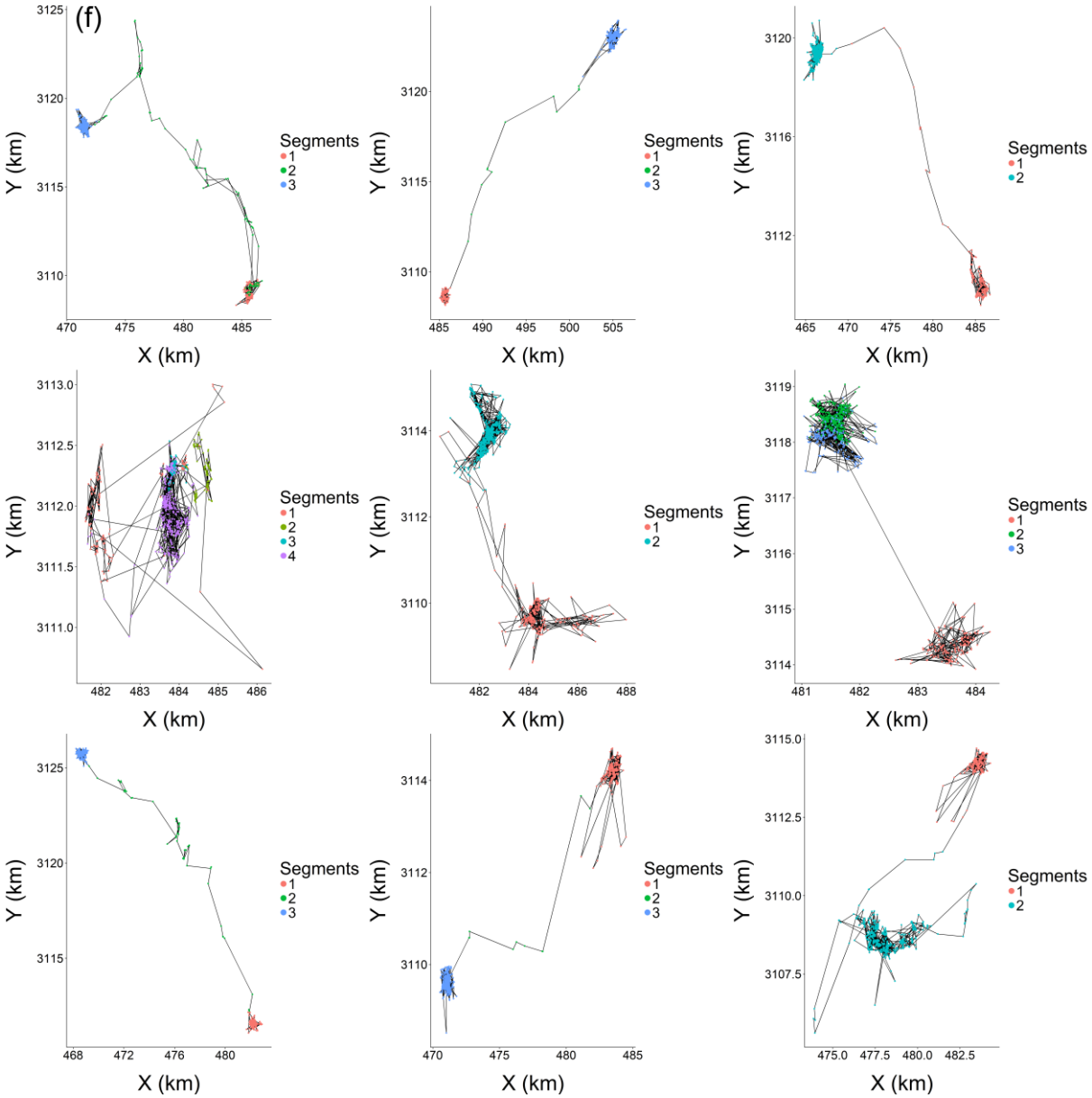

(f)
Y (km)
X (km)
Segments
1
2
3
4

Table A8 : Mean duration (± sd) of segments for each dispersal tactic identified (N classic dispersers = 49; N progressive dispersers = 14; N explorers = 62; N multi-ranger = 9; N strict philopatrics = 4; N aborted dispersers = 9) – N (sample size) is the number of individuals used to calculate the mean durations for each dispersal tactic and segment.

Dispersal tactic	Segment	Mean duration (days)	Standard deviation	N (sample size)
Classic disperser	1	75.7	33.4	49
	2	92.5	92.1	49
	3	134.5	86.9	33
	4	95.8	85.5	5
	5	17.0	NA	1
	6	15.0	NA	1
Progressive disperser	1	76.4	45.4	14
	2	133.1	76.8	14
	3	105.1	75.1	8
	4	13.0	17.3	2
	5	101.0	NA	1
Explorer	1	87.9	49.4	62
	2	60.7	51.4	59
	3	81.5	55.4	50
	4	42.5	32.8	27
	5	70.1	52.3	14
	6	22.0	8.5	2
	7	37.0	NA	1
Multi-ranger	1	71.1	39.4	9
	2	48.2	28.3	9
	3	61.6	50.9	9
	4	45.6	30.8	6
	5	106.5	46.0	3
Strict philopatric	1	66.8	36.3	4

	2	60.5	57.1	4
	3	169.8	NA	1
Aborted disperser	1	79.3	29.6	9
	2	58.0	50.2	9
	3	114.0	40.8	9
	4	33.2	28.6	5
	5	118.0	NA	1

Table A9: Mean departure date (± sd) from each segment for each dispersal tactic identified (N classic dispersers = 49; N progressive dispersers = 14; N explorers = 62; N multi-ranger = 9; N strict philopatrics = 4; N aborted dispersers = 9) – N (sample size) is the number of individuals used to calculate the mean durations for each dispersal tactic and segment.

Dispersal tactic	Departed segment	Mean date	Standard deviation (in days)	N (sample size)
Classic disperser	1	20th April	28.3	49
	2	25th May	57.8	33
	3	8th June	44.5	5
	4	7th November	NA	1
	5	24th November	NA	1
Progressive disperser	1	14th May	76.1	14
	2	25th June	69.6	8
	3	14th July	78.0	2
	4	30th July	NA	1
Explorer	1	2nd May	59.0	59
	2	9th June	66.7	50
	3	15th July	57.7	27
	4	12th August	48.3	14
	5	20th July	16.8	2
	6	6th August	NA	1
Multi-ranger	1	01st April	42.9	9
	2	20th May	56.6	9
	3	4th July	58.3	5
	4	23rd September	8.0	2
Aborted disperser	1	2nd May	25.1	9
	2	29th June	63.5	9
	3	26th September	46.5	5
	4	25th August	NA	1

Appendix IV: Environmental variables and their representation in each dispersal tactic

Figure A3: Plot of the first and second principal components and the proportion of the total variance explained from the PCA of landscape structure in the natal range. The PCA contains three centred and scaled landscape descriptors: nutritional quality indexed as the proportion of crops and meadows in the natal range; level of landscape heterogeneity indexed as the mean Shannon index value in the natal range; and level of human-related disturbance indexed as the mean distance to the nearest anthropogenic feature (road or building) within the natal range (high values of the descriptor 'disturbance' indicate a high distance to roads or buildings).

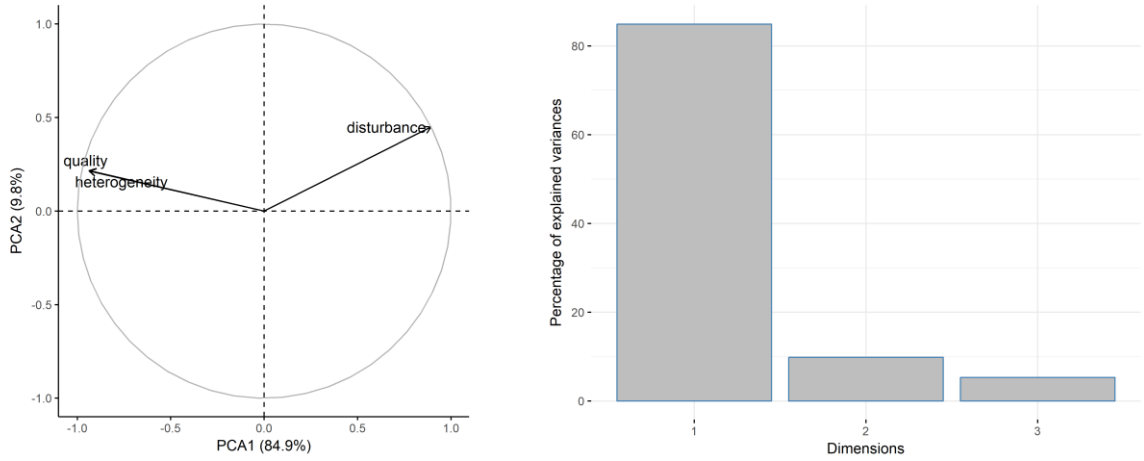


Table A10: Principal Component Analysis scores and proportion of variance explained by the three axes of the PCA on landscape characteristics of the natal range for 146 monitored juvenile roe deer.

Variable	**Axis 1**	**Axis 2**	**Axis 3**
Shannon index	34.4	15.5	50.1
Crop and meadow proportion	34.3	15.8	49.9
Distance to nearest anthropogenic feature	31.3	68.7	$3.95.\ 10^{-4}$
Eigenvalues	2.55	0.29	0.16
Cumulative Explained Variance (%)	84.9	94.7	100

Table A11: Mean phenotypic and landscape descriptors in the natal range (with their standard deviations) for each behavioural tactic identified during the dispersal phase – Classes: CD: Classic dispersers; PD: Progressive dispersers; E: Explorers; MR: Multi-rangers; P: strict Philopatrics; AD: Aborted dispersers. Descriptors: Bd_mass: body mass; Crop: Proportion of crops and meadows in the natal range; Shannon: mean Shannon index value based on the proportions of different habitat types in the natal range; Anthro_dist: mean distance to the nearest anthropogenic feature in the natal range (road or building); sd_x : standard deviation associated with a given descriptor, x. Female proportion = Proportion of females in a given class.

Class	Bd_mass (bm)	sd_bm	Crop (c)	sd_c	Shannon (s)	sd_s	Anthro_dist (ad)	sd_ad	Female proportion (%)
CD	17.02	1.70	0.90	0.23	1.75	0.31	183.21	71.10	61.20
PD	16.67	2.33	0.75	0.31	1.46	0.44	232.32	97.71	35.70
E	16.28	2.12	0.72	0.36	1.42	0.54	270.03	156.43	51.60
MR	15.56	2.33	0.61	0.37	1.30	0.67	277.14	145.11	44.40
P	14.78	2.13	0.57	0.32	1.45	0.52	237.03	127.10	75.00
AD	16.72	1.96	0.72	0.43	1.39	0.68	287.32	155.96	55.50

Appendix V: Assessing the robustness of our classification

To evaluate the relevance of our classification, we conducted an exploratory post hoc analysis of inter- and intra-individual variation in movement behaviour across tactics using continuous-time stochastic movement models (CTSMM, see Calabrese et al. 2016). The objective was to assess whether individuals were consistent in their spatial behaviour over time within and across tactics.

First, using the Ctmm package developed by Calabrese et al. (2016), we fitted Ornstein-Uhlenbeck models to individual monthly tracks and extracted three movement parameters: tau measures the position autocorrelation time and is interpreted as the home range crossing time (or the inverse of the attraction force) and D is a diffusion coefficient representing the rate of increase of the mean squared displacement over time. Sigma measures the movement variance (scaling to home range size) and is estimated using the values of tau and D through the following formula: $sigma^2 = D^2 * tau / 2$ (see Calabrese et al. 2016 for more details).

Then, to evaluate the degree to which individuals were consistent in their spatial behaviour over time for a given tactic, we estimated individual repeatability of these parameters for each of the dispersal tactics (package "rptR" in R – Stoffel et al. 2017). The repeatability models included month as a fixed effect as well as the identity of the individual as a random effect on the intercept in order to measure the adjusted individual repeatability (Stoffel et al. 2017). Movement behaviour was significantly repeatable for most of the 15 parameter-tactic (5 tactics * 3 parameters) combinations (12 out of 15), with repeatability values that ranged from 0.10 to 0.56 (Table A12). Although these repeatability values are moderate, averaging around 0.3, they are consistent with previous estimates for repeatability of movement and, more generally, most behavioural traits (Bell et al. 2009; Garamszegi et al. 2009; Hertel et al. 2019). Note that temporal repeatability was much lower for classic dispersers (0.02 to 0.10) due to the short-lived and abrupt modification of movement behaviour during long-range dispersal transience. These results, hence, indicate that, for a given tactic, individuals are consistent in their movement behaviour over time.

Second, we assessed whether our classification reliably discriminated between alternative dispersal tactics by evaluating inter- and intra-tactic variation in these three movement parameters. For each individual monthly track, we computed a measure of heterogeneity for each parameter. In other words, we wanted to see if there was any consistency in among-tactic differences of each parameter across the monitored months. We used a z-value measure for this purpose by applying the following formula: z.mvtpar = (max(mvtpar)-mean(mvtpar))/sd(mvtpar) (where mvtpar is tau, sigma or D, max(mvtpar) is the maximum value of the parameter reached during the individual monthly track, mean(mvtpar) is the mean value of the parameter across the same track and sd(mvtpar) is the standard deviation of the parameter across the track). Hence, a low z.mvtpar means that there is no significant fluctuation (or peaks) in parameter values (homogeneity) across the monitored months, and a high z.mvtpar means that there are some high fluctuations of values (heterogeneity). We then tested whether these z values were repeatable within a given tactic. Repeatability models contained the assigned tactic as a random effect and considered individuals as repetitions (package "rptR" in R – Stoffel et al. 2017). We found moderate but significant values of repeatability for sigma and tau (0.24 ± 0.13 – $p < 0.0001$ and 0.36 ± 0.16 – $p < 0.0001$ respectively), but not for D (0 ± 0.024 – $p = 1$). Indeed, D represents the mean squared displacement which does not encompass any notion of home range, but rather is based on distance travelled and hence likely poorly discriminates between alternative dispersal tactics (several alternative tactics had very similar straight line distances between the initial and final segment centroids – see Results section). On the contrary, tau and sigma are related to home range size and stability, and thus might better reflect behavioural changes in space use. Thus, according to these statistics, the tactics we identified appear moderately robust (with respect to two mechanistic movement parameters) and individuals are classified into ecologically meaningful groups.

Table A12: Repeatability models for each class and each movement parameter (tau, sigma and D). Strictly philopatric individuals and explorers were pooled in these analyses. Each model includes month as a fixed effect as well as the identity of the individual as a random effect on the intercept. Repeatability values above 0.2 are highlighted in bold.

Dispersal tactic	Parameter	R ± SE	p-value
Classic dispersers	Tau	0.03 ± 0.026	p =0.11
	Sigma	0.02 ± 0.025	p = 0.248
	D	0.10 ± 0.037	p = 0.000663
Explorers	Tau	0.17 ± 0.036	p = 4.06e-09
	Sigma	**0.32** ± 0.057	p = 5.12e-25
	D	0.14 ± 0.038	p = 6.05e-07
Progressive dispersers	Tau	**0.23** ± 0.096	p = 0.000485
	Sigma	**0.35** ± 0.1	p = 8.04e-08
	D	**0.29** ± 0.09	p = 2.12e-05
Multi-rangers	Tau	**0.33** ± 0.155	p = 0.00445

	Sigma	**0.56** ± 0.162	p = 4.18e-07
	D	**0.25** ± 0.136	p = 0.00911
Aborted dispersers	Tau	0.04 ± 0.054	p = 0.335
	Sigma	0.13 ± 0.107	p = 0.0421
	D	**0.27** ± 0.118	p = 0.000552

References for this Appendix V:

Bell, A. M. et al. 2009. The repeatability of behaviour: a meta-analysis. – Animal behaviour 77: 771–783.

Calabrese, J. M. et al. 2016. ctmm: An R package for analyzing animal relocation data as a continuous-time stochastic process. – Methods in Ecology and Evolution 7: 1124–1132.

Garamszegi, L. Z., et al. 2009. Changing philosophies and tools for statistical inferences in behavioral ecology. – Behavioral Ecology 20: 1363–1375.

Hertel, A. G., et al. 2019. Don't poke the bear: using tracking data to quantify behavioural syndromes in elusive wildlife. – Animal Behaviour 147: 91-104.

Stoffel, M. A. et al. 2017. rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. – Methods Ecol. Evol. 8:1639–1644.

Chapter IV:

Dispersing in risky environments: effects of increased costs of dispersal on the evolution of transfer traits

Authors : Delphine Ducros[1,2], Stephen Palmer[3], Mark Hewison[2], Nicolas Morellet[2], Justin Travis[3], Aurélie Coulon[1,4]

Affiliations :

1 Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle, Centre National de la Recherche Scientifique, Sorbonne Univ., CP 135, 57 rue Cuvier, FR-75005 Paris, France

2 CEFS, Univ. de Toulouse, INRA, Castanet-Tolosan, France

3 School of Biological Sciences, University of Aberdeen, Aberdeen AB24 2TZ, U.K

4 CEFE, CNRS, Univ. Montpellier, EPHE, IRD, Montpellier, France.

Introduction

Dispersal is at the core of species dynamics and is fundamental for population ecology through its association with many biological processes (genetics, demography, biological invasions, species adaptation and interactions, etc.) (Ronce 2007, Clobert et al. 2012). This process allows individuals to reach new environments, potentially providing dispersers with mates, resources, or escape bad environmental conditions (Ronce 2007). It can also alleviate competition if individuals are settling in a lower density habitat compared to their natal range, or limit inbreeding if the distance between their natal and settlement ranges is above the range of relatedness (Ronce 2007). Additionally, in the context of environmental change, dispersal may also provide benefits to dispersers, such as keeping track of climate change or escaping disturbance (Watkinson and Gill 2002, Bowler and Benton 2005). Many factors determine if individuals will disperse, such as sex, weight, age, environmental conditions, etc., and thus, dispersal is considered to be a condition-dependent process (Clobert et al. 2012), leading to both philopatric and dispersing individuals within a population. This balance between philopatry and dispersal then acts on species dynamics, in link with the fitness of each individual (Greenwood 1980, Li and Kokko 2018). However, dispersing also entails costs, which are of four types: energy, risks, time and opportunity (Bonte et al. 2012). These costs are tightly linked to

both the environmental conditions experienced by dispersers and their actual movements, and they can occur during the three phases of dispersal (emigration, transfer and settlement).

We are currently facing major changes in environmental conditions (Vitousek et al. 1997, Foley et al. 2005, Dawson et al. 2011, IPCC 2014), which may restrict the access to important resources for many species (Backlund et al. 2008) and increase mortality risks associated to movement. For example, the construction of dense road networks, human activities and urbanisation may lead to more road kills, in particular if individuals are moving into an unfamiliar place (e.g. in American martens, Johnson et al. 2009). For these reasons, we expect that dispersal costs may increase with global changes (Bonte et al. 2012). This increase should modify the balance between the costs and benefits of dispersal and trigger the selection of new strategies or of modifications of current dispersal strategies, which allow reduced costs of dispersal (Bonte et al. 2012, Travis et al. 2012). Indeed, previous empirical and theoretical work showed that an increase in costs impacts current dispersal strategies and will also shape dispersal evolution (Bonte et al. 2008, 2012, Dytham 2009, Travis et al. 2012, Tanaka 2016).

Indeed, dispersal has a genetic basis and as such, each of its phases is under selection to maintain a favourable costs/benefits ratio (Bonte and Dahirel 2017, Saastamoinen et al. 2018). Global changes are hence expected to influence the way selection may act on dispersal traits to maintain the balance between costs and benefits at a favourable level and trigger evolutionary responses from dispersal traits. Previous work addressing the potential evolutionary consequences of global changes on dispersal (Hein et al. 2004, Gros et al. 2006, Poethke et al. 2011) has focused on the evolution of a dispersal kernel. These studies showed that the travelled distance is expected to be reduced when costs increase because individuals target the closest suitable patch from their initial habitat to decrease dispersal costs, which, as a consequence, leads to faster settlement (Hein et al. 2004, Gros et al. 2006, Poethke et al. 2011). Research also showed that dispersal may evolve reduced dispersal propensities and more correlated movement paths in the context of habitat fragmentation or degradation (Travis and Dytham 1999, Gros et al. 2006, Kun and Scheuring 2006, Schtickzelle et al.

2006, Cheptou et al. 2008, Poethke et al. 2011, Henriques-Silva et al. 2015). Some recent studies have also begun to investigate the evolution of the transfer phase using models that explicitly represent the movement process, i.e. using the three dispersal phases. For plants, it has been shown that, following habitat loss, plants are expected to exhibit either evolutionary rescue or evolutionary suicide (Travis et al. 2010). This arises because plant height may either become higher or lower, leading to either long-distance dispersal and colonisation of new patches, or no dispersal and local patch extinction. For animals, movements may evolve towards shorter paths when transfer costs increase, through the strengthening of the bias individuals have towards the closest suitable patch as soon as an individual emigrates (Bartoń et al. 2009). Several studies also confirmed that movement paths should follow a more correlated walk when risks increase, therefore reducing the amount of steps an individual will take in a hostile environment and the associated costs (Bartoń et al. 2009, Travis et al. 2012). However, although these studies offer some initial insights into how selection may operate on processes impacting the transfer phase of dispersal, they have utilised highly simplified movement models (but see Henriques-Silva et al. 2015) and have explored results for relatively small volumes of the parameter space. In particular, studies have not elucidated how the evolution of movement rules will vary as a function of emigration rules, and how this depends upon the cost of movement. As a consequence, knowledge about the exact process by which individuals move in a risky environment and the evolutionary mechanisms behind it (i.e. which dispersal traits are selected and why) is still lacking, especially in the context of environmental changes (Holyoak et al. 2008, Gibbs et al. 2010) that are likely to impact dispersal costs (Bonte et al. 2012). This may have important implications, as dispersal strategies that evolve under global change will be based on the evolution of these dispersal traits, and adaptation potential should largely depend upon the maintenance of the diversity in dispersal associated traits within populations (Byers 2005, Eizaguirre and Baltazar-Soares 2014).

Therefore, in this study, we used an individual-based model to infer the effects of increased transience mortality costs on the evolution of two transfer traits, and do so for a broad range of

emigration behaviours. These transfer traits are dispersal bias, which represents the tendency of an individual to move away from its natal area; and directional persistence, which controls the tendency of an individual to follow an auto-correlated path. We expected that increased risks of mortality during dispersal would select for tactics in which settlement occurs faster. This translates into two main mechanisms: (i) more tortuous trajectories, i.e. displaying a lowered directional persistence, should allow for more frequent changes of direction and hence a more likely detection of a suitable habitat; (ii) reduced dispersal biases, which make individuals to be less driven to disperse far away from their natal habitat should allow a reduction of the time spent in the matrix. However, too low directional persistence or dispersal bias might not be beneficial either, because they would prevent individuals from reaching potential suitable habitats (for example if this habitat requires the individual to consistently go towards a given direction, or if the habitat is too far from the natal range to be reached by an individual having a low dispersal bias). Thus, we expected both traits to stabilise around a threshold value that would optimise both the need to move away from the natal area, and the need to divert from the initial direction taken at emigration and settle if a suitable habitat is found. Finally, we expected that both reductions in directional persistence and dispersal bias would lead to decreased dispersal distances. Because previous work indicated that the degree of hostility of matrix cells influenced dispersal trajectories (Baguette and Van Dyck 2007, Bartoń et al. 2009), we expected that resistance to movement should impact dispersal evolution. Therefore, we varied the degree of hostility of matrix cells, and determined its effect on the evolution of transfer traits. Considering the interplay between dispersal traits, we expected our results to change for different emigration probabilities (Travis et al. 2012); indeed, higher dispersal propensities might be associated with a faster evolution of dispersal traits, and the best dispersal strategies species-wise might be different depending on the size of the fraction of the population that disperses. Therefore, we also varied emigration probability between simulations.

Material and methods

a. Modelling approach

Simulations were run using the software Rangeshifter (RS), a platform for implementing spatially-explicit individual-based models. RS allows for modelling eco-evolutionary dynamics and integrating a specific implementation of each of the three phases of dispersal (Bocedi et al. 2014). In particular, the transfer phase can be described using the SMS method (Palmer et al. 2011), which allows for step-by-step determination of the movement path based on characteristics of the environment within the perceptual range of the individual, and on movement rules regarding trajectory straightness/directionality.

In RS, the environment is represented by a raster composed of cells either suitable or unsuitable for settlement; each type of cell is also associated with an attraction value[3]. Individuals are characterized by a set of demographic and dispersal parameters. Demographic parameters include the type of sexual model implemented in RS (asexual, sexual or complex sexual model), an intrinsic growth rate, the proportion of males and females, the number of reproductive seasons per year, a competition coefficient and a carrying capacity (See Table 1). Dispersal parameters are specific to each of the three phases of dispersal. Emigration is described by the probability to disperse, settlement by the probability to settle, and the transfer phase is modelled using four different traits. Directional persistence (DP) represents the directional consistency in movement, i.e. the auto-correlation in the successive angles of the movement steps. Dispersal bias (DB) describes the propensity an individual has to move away from its natal habitat at departure. Visual representation of the effects of these two traits is provided in the Supplementary Materials Annex I. To represent the fact that the propensity to disperse far from the natal habitat decreases as the individual moves away, DB is

[3] The attraction value in this manuscript corresponds to the parameter named “matrix costs” in RS, i.e. the degree of hostility of matrix cells. These “matrix costs” represent the relative resistance to movements of the different matrix cells. However, they are not directly related to the dispersal costs we wished to implement, i.e. mortality risk costs. Thus, to avoid any misunderstanding, we preferred in this manuscript to use the term “attraction”, which conveys the same idea that some cells may be preferred when moving into the landscape, because they oppose less resistance.

described using a sigmoid function having the two parameters AlphaDB and BetaDB. AlphaDB characterises the slope coefficient of the function and BetaDB the number of steps realised at the inflexion point of the curve representing the decrease in DB.

A run consists in the launching of a given number of individuals into initial locations of suitable cells of the landscape, which may attempt to disperse or not. Dispersing individuals have a maximum number of steps they can take. At each step of the run, all individuals may move in one of their eight neighbouring cells, based on their respective values of DP, DB, memory size (i.e. the number of passed steps over which to calculate the current direction to apply DP), and on the suitability of the cells within their perceptual range in each of the eight directions (the number of cells away from their current cell for which individuals can perceive the characteristics) (See Supplementary Materials Annex II). Moreover, at each of those steps, individuals may die based on a per-step mortality probability. If individuals reach a suitable cell (i.e. do not die in the process of dispersing or do not run out of steps before having reached a suitable cell), they may reproduce and transmit their genome to the next generation. After that, they die and the next generation follows the same steps. The run is set for a particular duration (for example, 10 000 years), and thus, it ends when this duration is attained.

Dispersal may be beneficial for three main reasons in RS. First, it allows individuals to colonise more habitat cells. Because suitable cells go extinct at a given probability, selection should favour individuals which disperse because only them may survive if the cell they came from goes extinct. Secondly, a carrying capacity is implemented in RS. Thus, individuals which disperse and settle in a low-density cell may perform better than individuals whose cell density may attain carrying capacity. Thirdly, kin selection favours dispersers which move some distance away from their natal site, as, by doing so, they are less likely to be competing with their near relatives.

Lastly, the evolution of dispersal traits (as well as demographic traits) is enabled through a genetic implementation of dispersal. Indeed, each dispersal trait is coded by one chromosome, and

corresponding alleles were positioned on four loci in our experiment. These loci are subjected to mutations, and they may also allow for crossovers, which bring some variability in the phenotypes expressed by dispersers. At the beginning of a run, individuals may express a variety of movement characteristics during dispersal, determined by a mean value of each of the four transfer traits and their initial standard deviation in the population. Thus, selection should favour some phenotypes depending on environmental conditions, which means the corresponding trait characteristics will be transmitted to the next generation, based on the value of the trait of parents (mean value of the trait) and a scaling factor specific to this trait. The scaling factor describes how large a change on the allelic scale from the parent to offspring genome will be on the phenotypic scale. Each of the aforementioned traits is thus described using a mean value, a standard deviation and a scaling factor in the population when initiation a run.

b. Simulation experimental plan

Our objective was to model the effect of increases in the mortality costs of dispersal on the evolution of dispersal transfer traits.

To do so, we used a hypothetical species living in a fragmented landscape for which suitable and unsuitable habitats are disjointed and can be clearly identified. Unsuitable cells will be thereafter named ‘matrix’. We hence worked on a grid landscape described in Table 1. Species demographic parameters were chosen to be representative of a species with relatively high growth rate and no sex bias in the population, and are also described in Table 1. Individuals were allowed to disperse from a suitable cell or remain philopatric based on the following initial dispersal rules and experiment plan. However, once dispersal started, individuals were not allowed to return and settle in their natal patch.

Table 1: Summary of base demographic and landscape parameters values for modelling transfer traits evolution.

Species parameters	
Model	Simple sex
Generation	Discrete
Sex ratio	0.5
Competition coefficient	1
Intrinsic growth rate	6
Number of reproductive seasons / year	1
Initial population size in each cell	150
Carrying capacity	150
Landscape parameters	
Dimensions	100*100
% of suitable cells	5
Local extinction probability	0.05

Our experimental design was set to address how mortality risks during transfer (four levels tested) affect the evolution of four transfer traits, depending on emigration rate in the population (six levels tested) and the level of attraction of habitat cells (five levels). We assessed the robustness of our results to initial conditions by testing three sets of initial values of DP, GB, AlphaDB and BetaDB (See Table 2).

Transfer traits were modelled using three sets of initial values (see Table 2) from which traits were allowed to evolve. These sets intended to reflect different dispersal tactics, in which individuals may present more tortuous dispersal and low dispersal bias (set 1) or strongly biased movement away from the natal area and highly correlated movement (set 3). Set 2 contained dispersal trait values that reflect intermediate movement tendencies compared to the two other sets. We fixed perceptual range to 3 cells in all our simulations. Memory size was also fixed to 3 in all simulations (meaning that individuals could keep their tendency to move in a given direction for a longer period of time by remembering the past three cells it travelled in, compared to individuals that would only remember the past cell). Because our study focused on the evolution of transfer traits, within a simulation

emigration and settlement probabilities were fixed and density-independent. Settlement probability was set to 1 if an individual found a suitable cell. To assess the effect of emigration rates on the evolution of transfer rules, we ran each set of parameters with emigration probabilities varying from 0.1 to 0.6, in 0.1 increments.

To study the effects of increased dispersal costs on the evolution of dispersal, we ran the different combinations of sets of parameters and emigration rates with different per-step mortality probabilities: 0.005, 0.01, 0.05 and 0.1. This risk probability applied as soon as an individual moved out of its natal cell, and lasted until it reached a suitable cell or died. Additionally, we varied attraction values associated to the matrix cells of the landscape, while the attraction value of suitable cells was always set to 1, which allowed us to model the level of attraction an individual had for a suitable cell. Attraction was set to the following relative values: 10, 50, 100, 150 and 500.

Table 1: Sets of initial trait values used in the experiments. We provide the mean trait value in the population as well as its standard deviation (Sd). The scaling factor (Sf) is also provided, which describes how large a change on the allelic scale translates on the phenotypic scale.

Parameters	Set 1	Set 2	Set 3
Directional persistence	Mean : 2 Sd : 1.5 Sf : 1.5	Mean : 4 Sd : 1.5 Sf : 1.5	Mean : 6 Sd : 1.5 Sf : 1.5
Dispersal bias	Mean : 2 Sd : 1 Sf : 1	Mean : 3 Sd : 1 Sf : 1	Mean : 1 Sd : 1 Sf : 1
AlphaDB	Mean : 1 Sd : 1 Sf : 1	Mean : 0.5 Sd : 1 Sf : 1	Mean : 0.25 Sd : 1 Sf : 1
BetaDB	Mean : 5 Sd : 5 Sf : 5	Mean : 10 Sd : 5 Sf : 5	Mean : 15 Sd : 5 Sf : 5

Dispersal traits were allowed to evolve for 10 000 years. We simulated each combination of emigration probability, per-step mortality probability, levels of attraction and initial sets of parameters, and replicated each simulation 10 times. In total the experiment plan represented 3600

simulations (10 replicates*3 sets*4 per-step mortality probabilities*5 attraction values*6 emigration probabilities).

For each simulation we recorded the mean values of traits in the population at a given year every 200 years, and every 200 years during the last thousand years (i.e. after equilibrium had been reached) individual dispersal traits, status (philopatric, successful disperser, failed disperser), distance (i.e. the Euclidean distance from departure to arrival cell) and the number of steps travelled (the latter only for dispersing individuals).

c. Analysing dispersal evolution

As a first step, we analysed the values reached by traits at the end of the simulation for all simulation conditions to determine whether populations reached a stable strategy or not. This step mainly consisted in evaluating visually how traits evolved with time and if they did reach an equilibrium value, i.e. a stable value. Moreover, this first step allowed us to evaluate the strength of the selection pressure exerted on each trait by mortality risk, in link with other simulation factors. A fast evolution leading to the stabilisation of a trait would imply a strong selection on that trait.

Second, we partitioned the variance in each dispersal trait to determine the relative contribution of each simulation parameter on the evolution of dispersal traits. We centered and scaled each simulation parameter prior to fitting anova models describing each trait in relation to attraction, per-step mortality, emigration probability and sets of initial trait values using the package 'stats' in R (R Core Team 2019). We calculated the percentage of explained variance by a given parameter (or interactions between several parameters) for each transfer trait at equilibrium (last 1000 years). We then compared the relative contribution of each of these parameters on the observed variations in dispersal traits.

To interpret our analyses, we only kept the simulation parameters that were identified as accounting for at least 5% of the variance in a given dispersal trait. Because we wished to assess the long-term consequences of increased dispersal costs on dispersal trait evolution, and consequently on actual

dispersal movement and success, we also extracted distances and number of steps travelled after 10 000 years of evolution and the dispersal success rate.

Results

1. Equilibrium strategies

Most traits in the 3600 experiments reached equilibrium values by the end of the simulations (see examples in Supplementary Section - Annex III). However, for some combinations of traits and conditions, like DP in set 3 or DB in set 1, stabilization was not reached yet at the end of the simulation, but the trait showed a weakly decreasing slope and we can presume these traits would reach equilibrium if simulations were ran for a longer period of time. Only one trait, BetaDB in set 3, does not seem close to reach equilibrium. We can also note that equilibrium was reached faster when emigration probability was high, especially for DB.

DP evolved towards similar values in sets 1 and 2, but not in set 3 where the trait was still evolving at the end of the simulations (Annex III, fig. S4a). This probably occurred because the initial value for DP for set 3 was the highest. However, we can expect that if we ran the simulation for a longer period of time we may reach similar values for the set 3 as well. Without consideration of the variations in mortality or attraction, DP evolved towards a mean value of 1.75 ± 0.001 (over all combined runs, i.e. without distinguishing the different values of mortality or attraction combined), indicating a rather low DP, although movements are still slightly correlated. DB only reached equilibrium in set 3, and evolved to a mean value of 1.00 ± 0.00008, indicating there was essentially no DB in the population after 10 000 years (Fig. S4b). In sets 1 and 2, equilibrium was not yet attained probably because initial values in sets 1 and 2 were higher compared to set 3, but as for DP, we may expect that similar values may be reached for longer simulation durations. AlphaDB decreased from its initial values in all simulations, but not identically between sets: this trait decreased from its initial value for the first two sets, and stabilised around 0.91 ± 0.001 or 0.32 ± 0.0007 for sets 1 and 2 respectively. At the end

of the simulation, AlphaDB remained stable in set 3, taking values between 0.27 ± 0.001. This result indicates that initial values had a strong influence on the evolution of AlphaDB, contrary to the other parameters (Fig. S4c). Lastly, BetaDB reached equilibrium for sets 1 and 2, but not set 3. Values reached were not identical between sets either (between 3.34 ± 0.006 for set 1 and 6.02 ± 0.006 for set 2), indicating again that initial values had a strong influence on the evolution of BetaDB (Fig. S4d). In set 3, because DB evolved very quickly to a mean value of 1, there was overall no DB in the population at the end of the simulation, which may have led to low selection pressure on BetaDB for that set and no evolution towards a particular value.

2. Variance analysis

Per-step mortality probability contributed importantly to the observed variance in DP (17.4 to 44.1% of variance explained - see table 2). Moreover, attraction was also responsible for 7.9 to 15.5% of the total variance in DP, and interacted in sets 1 and 2 with per-step mortality probability to influence DP (between 7.0 to 7.3% of explained variance for DP). Lastly, the different sets of initial trait values also had a strong influence on values reached by DP at the end of the simulation, with 21.5% of the total variance explained by the initial DP values. DB also varied with per-step mortality, with 5.6 to 24.1% of variance explained by this metric. Additionally, DB appeared to be strongly influenced by emigration probability (5.2 to 22.1 of variance explained), and the interaction between emigration probability and per-step mortality probability also influenced DB in set 1. On the contrary, mortality did not appear to have strong effects on AlphaDB. Attraction did have an effect on the evolved values of AlphaDB, with 6.1 to 24.0% of total variance of AlphaDB explained by this parameter. The initial set of values taken by AlphaDB also influenced the values reached at the end of the simulation (40.2% of total variance). Similarly, mortality has no strong effect on BetaDB, but attraction seemed to influence BetaDB with approximately 37.2 to 42.8% of explained variance by this parameter. Finally, the different sets of initial BetaDB values also had a strong influence on values reached by traits at the end of the simulation (explained variation of 78.9%).

Table 2: Percentage of explained variance of each dispersal trait by four simulation factors and their interactions. The analysis of variance was performed for each set separately and combined, as reported in the column 'set'. Only percentages of explained variance above 5% are reported. Values above 10 % are written in red.

Dispersal trait	Simulation set	Attraction	Per-step mortality probability	Emigration probability	Initial set of parameters	Attraction*per-step mortality probability	Per-step mortality probability *emigration probability
DP	1	15.5	44.1		-	7.0	
	2	7.9	36.3		-	7.3	
	3	9.9	17.4	41.2	-		
	All sets	5.8	14.5	8.9	21.5		
DB	1		21.2	22.1	-		7.2
	2		24.1	20.6	-		
	3	5.9	5.6	5.2	-		
	All sets		10.4	9.4			
AlphaDB	1	6.1			-		
	2	24.0			-		
	3	(none)			-		
	All sets	5.0			40.2		
BetaDB	1	37.2	6.8		-		
	2	42.8			-		
	3	(none)			-		
	All sets				78.9		

3. Effects of mortality risks on the evolution of dispersal traits

DP and DB both evolved towards lower values when per-step mortality increased, for all conditions of emigration probability, attraction and sets (Example of the variations between DP and DB with increasing mortality are provided in fig. 1 and 2 – Variations for all simulation conditions are provided in the Supplementary Materials Annex IV, figs. S5 to S7). For high mortality rates both the DB and DP evolved towards values close to 1, which is the lowest value those parameters can take. Our prediction of an intermediate value for DB and DP was hence not fulfilled. Instead, enhanced risks triggered the evolution towards rather tortuous and unbiased trajectories. Moreover, when attraction was higher, DP and to a lesser extent DB (only for set 3) remained higher compared to when attraction was low, leading to more correlated and biased movements away from the natal area when individuals could better discriminate between suitable and unsuitable cells (fig S5 and S7c). For all combinations of conditions, the simulations performed with the lowest level of attraction showed a slightly different pattern from the others, with a lower decline of DB and DP when mortality risks increased, and an outlier distribution within the overall pattern of decrease in the values of DB and DP when attraction increased. The decline in DB with increasing per-step mortality probability was steeper when emigration probability was higher, indicating that the effect of mortality was stronger when more individuals disperse (Fig. 2). A similar effect was found for DP, but only for set 3.

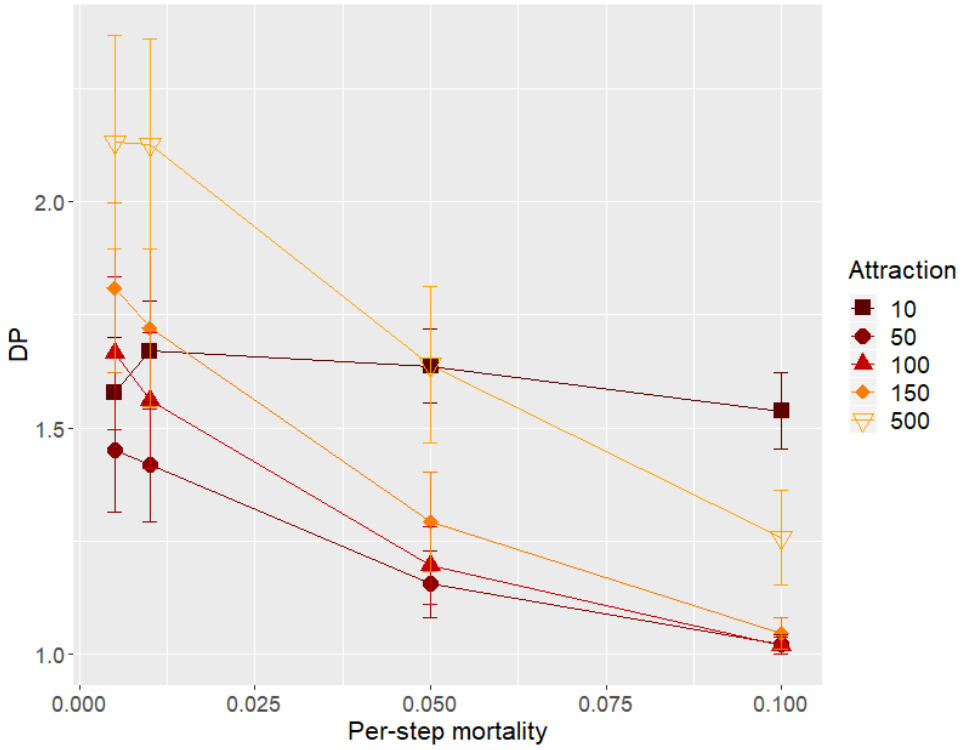


Fig. 1: Variations in mean DP averaged over the last 1000 years for increasing per-step mortality probability and varying levels of attraction. Values are given for the following simulation conditions: emigration probability = 0.1 and set of initial values = set 1.

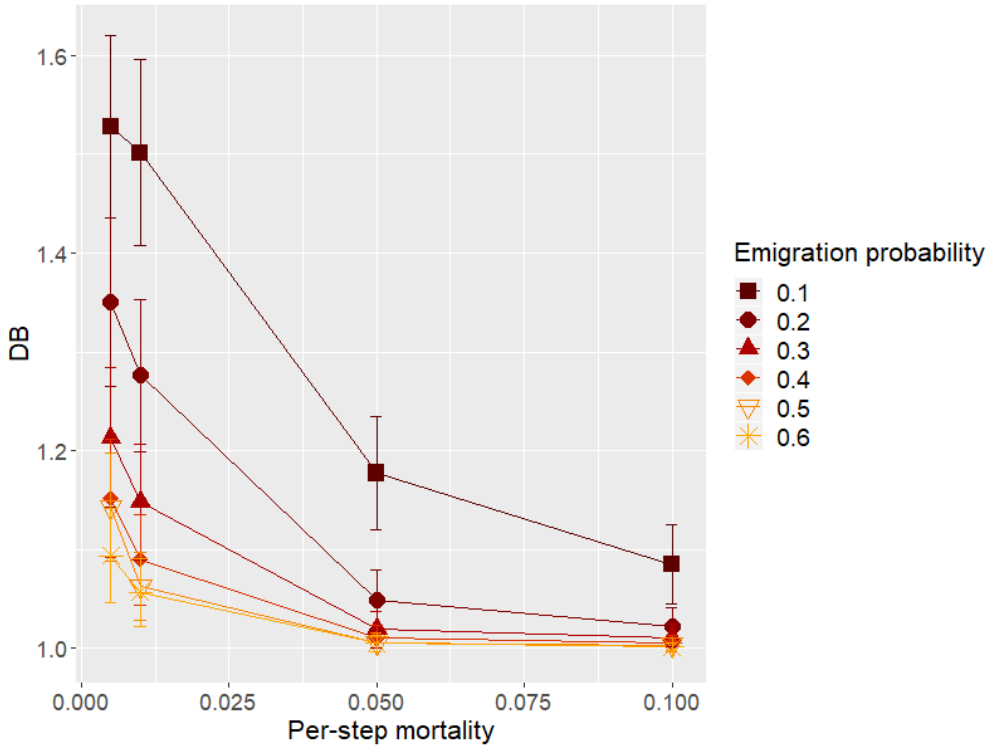


Fig. 2: Variations in mean DB averaged over the last 1000 years for increasing per-step mortality probability and varying levels of attraction. Values are given for the following simulation conditions: emigration probability = 0.1 and set of initial values = set 1.

AlphaDB and BetaDB did not present particular trends when mortality increased, except BetaDB which values were slightly lower for increasing per-step mortality probability for the set 1 only (see Supplementary Materials – Annex IV Fig. S8 and S10). However, these traits varied with attraction. BetaDB remained higher when attraction increased for sets 1 and 2 (for which a dispersal bias was still active until the end of the simulation, Fig. S10 and S11), while AlphaDB values tended to be lower when attraction increased for the two same sets (Figs. S8 and S9). This indicates that dispersal bias might persist longer during the dispersal event when attraction is high, driving individuals to move further away compared to when attraction is low. Emigration rate seemed not to have any effect on the mean values of AlphaDB and BetaDB (See Table 2).

4. Effects of mortality risks on dispersal outcomes

Dispersal distances from the departure to arrival cell decreased when mortality risks increased in all simulations (see one example Fig. 3). Additionally, increasing attraction led to even smaller values of dispersal distances. The same effects were observed for the number of steps (see Supplementary Materials – Annex V Fig S12). Thus, dispersers travelled less far and in fewer steps when mortality costs were higher, and even less if the contrast between suitable and unsuitable cells was stronger. Lastly and expectedly, the proportion of successful dispersers among all dispersing individuals decreased when per-step mortality probability increased (Fig 4). This effect was lower when attraction was higher, indicating that individuals perform better during dispersal when they can distinguish between suitable and unsuitable cells better.

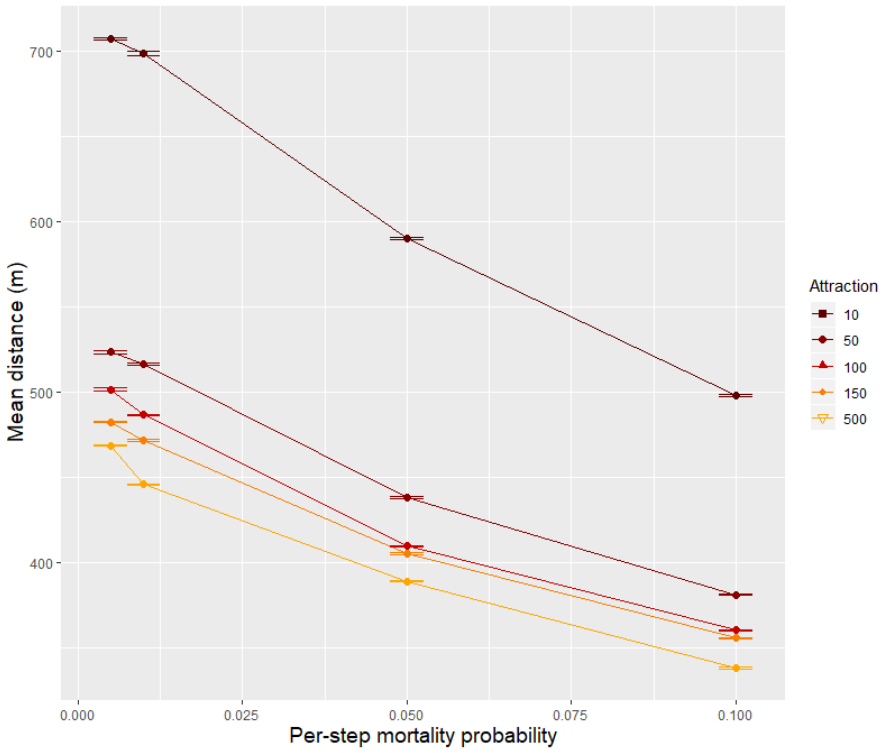


Fig. 3: Mean dispersal distances moved by successful dispersers averaged over the last 1000 years in relation to per-step mortality probability and attraction. Values are given for the following simulation conditions: emigration probability = 0.1 and set of initial values = set 1.

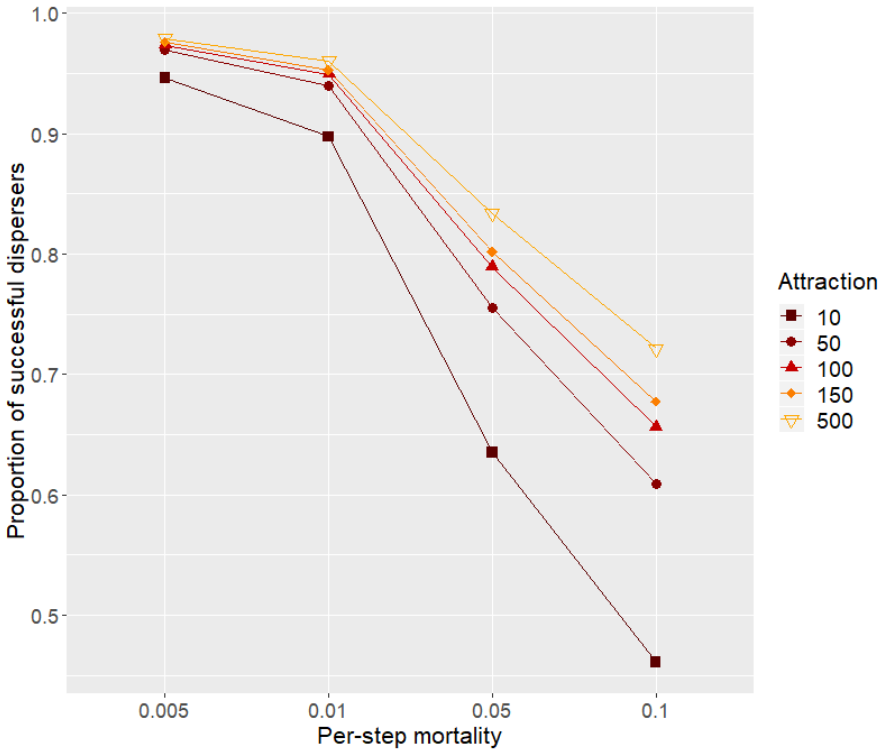


Fig 4: The mean proportion of successful dispersers averaged over the last 1000 years in relation to per-step mortality probability and attraction. Values are given for the following simulation conditions: emigration probability = 0.1 and set of initial values = set 1.

Discussion

In this work, our objective was to determine how dispersal traits may evolve with increasing transfer-associated mortality. We found that both directional persistence and dispersal bias decreased when mortality increased, and that this effect was stronger for reduced attraction or increased emigration probability for directional persistence and dispersal bias respectively. AlphaDB and BetaDB, which describe the decay of dispersal bias over the course of dispersal, did not vary much with mortality and did not appear to be under strong selection. These results predict that in riskier environments, evolution favours more tortuous dispersal trajectories, with a lower tendency to move further away from the natal range at each step, and consequently reduced dispersal distances.

Dispersal strategies evolve depending on the balance between costs and benefits (Bonte et al. 2012, Travis et al. 2012). Here, we purposely considered a rather harsh environment, with low habitat

suitability and increasing mortality risk during dispersal, in order to reflect the current massive habitat degradation which is occurring on the planet, and determine how dispersal might evolve when the equilibrium between costs and benefits becomes unbalanced. The most efficient way to escape mortality is to spend less time in the unsuitable matrix, and thus, settle fast after emigrating (Schtickzelle et al. 2006, Cornelius et al. 2017). In a harsh environment, successful dispersers are hence individuals that are able to settle fast, and thus close to their natal cell. To do so, they first need to be flexible in their movement to reorient it faster if a suitable cell is perceived, although this result may seem counter intuitive because one may expect that more tortuous movements lead to longer trajectories. Directional persistence and dispersal bias both evolved rather stable values, indicating individuals are mainly evolving towards one strategy which consists in reducing dispersal bias and directional correlation. Thus, high values of DP or DB might not be represented as much in the genomes anymore, leading to a decrease in adaptive potential (Hoffmann et al. 2017). In terms of phenotypes, these results are of capital importance because they suggest that individuals may lose their potential for long-distance correlated dispersal when too many risks incur during the transfer phase, which may have far-reaching consequences on population dynamics (Benton and Bowler 2012).

Indeed, dispersal strategies and population dynamics are known to be tightly linked (Bowler and Benton 2005, Benton and Bowler 2012). In particular, dispersal plays a major role in enhancing connectivity between populations, and gene flow (Stenseth and Lidicker 1992). For example, gene flow within a population is highly dependent on the distance travelled by dispersers (Slatkin 1987). Because dispersal distances decreased strongly when costs increased, we expect gene flow to be less important and more inbreeding in the long term. Short distances dispersed may also lead to more isolated populations (Johst et al. 2002). To fully demonstrate that adaptive potential for long-distance dispersal may be reduced or lost, additional experiments should include time-dependent risks, where in the first 5000 years of the experiment, risks are set to increase, and in the next 5000 years, risks are set to decrease. A stabilisation of directional persistence and dispersal bias at low

values throughout the entire experiment may provide evidence that the population may have lost its potential for long-distance dispersal. Moreover, fewer individuals dispersed successfully, and thus, these might not be able to play a role in rescuing populations or allowing gene flow. These effects of global changes on dispersal costs, and in turn, on gene flow and connectivity could have important implications for population functioning and persistence, with isolated, inbred and poorly connected populations, which may increase their risk of extinction. As a consequence, dispersal may not be as beneficial as it was before global changes occurred.

Growing research has demonstrated the importance of informed dispersal on dispersal strategies and success (Clobert et al. 2009, Delgado et al. 2014, Ponchon et al. 2015, Awade et al. 2017). By better making the difference between suitable or unsuitable habitats, through cues such as conspecifics' density, landscape cover or meteorological conditions, individuals can choose dispersal tactics that maximise their fitness (Clobert et al. 2009). Here, we show that the inclusion of increased attraction (which allows for a better contrast between suitable and unsuitable habitats) also influenced the evolution of dispersal traits, triggering higher evolved DP and, to a lower extent, DB. Indeed, when the attraction is high, individuals possessing a high DP should reach the suitable cell in fewer steps compared to an individual with low DP, and thus incur less risk to die in the unsuitable matrix (because less time is spent in a matrix where mortality is step-based) (Schtickzelle et al. 2006, Cornelius et al. 2017). Thus, their traits should evolve towards a higher capacity to go more efficiently towards suitable cells, i.e. realizing straighter movement paths, consistently with previous empirical or theoretical studies (Zollner and Lima 1999, Hein et al. 2004, Schtickzelle et al. 2006, Bartoń et al. 2009). However, for paths to become and remain straight, individuals first have to locate a suitable cell, which in our case, did not happen until such a cell is present within its perceptual range. For several studies from the literature, omniscient individuals or individuals possessing a bias towards a suitable cell were simulated in risky environments, and thus, they could orient their movement towards a suitable habitat as soon as they emigrated, which may have biased the evolution of dispersal traits in their simulations and could explain why we do not find the same results (Bartoń et

al. 2009, 2012). On the contrary, when attraction is low, only individuals with a low DP should be able to deviate from their initial trajectory if they perceive a suitable cell. This result is of great importance for population dynamics because it shows that depending on individual capacity to discriminate between suitable and unsuitable habitats, dispersal traits could evolve towards more or less tortuous trajectories or biased movements away from natal range, influencing the effect of dispersal on population functioning.

Moreover, understanding which selection pressures act on individuals is of primary importance to better comprehend eco-evolutionary processes (Schluter et al. 1991, Paranjpe and Sharma 2005, Futuyma 2009, Gogarten et al. 2012). In our study, AlphaDB and BetaDB did not vary much with simulation variables, except with the sets of initial trait values, suggesting these two traits might not be under strong selection, contrary to DP and DB, which strongly varied with per-step mortality risk and attraction for DP, and whose evolution towards stable values went faster when emigration increased. Thus, all movement traits are not equally affected by environmental pressures, which may have important implications in terms of population dynamics, especially if emigration and settlement traits were also subjected to evolution and interacting with transfer traits (Travis et al. 2012). Depending on the evolutionary force acting on selection (for example increased mortality risk or habitat attraction), and depending on the trait targeted by selection, movement paths, and thus population dynamics, should not be impacted the same way. For example, the reduction of emigration propensity by some environmental pressures (leading to very crowded populations and increased risks of evolutionary suicide or inbreeding, Gyllenberg et al. 2002, Nichols 2017) or emigration followed by either tortuous or correlated movements (leading to contrasted levels of mortality) may not have the same fitness implications (Bowler and Benton 2005, 2009, Brown et al. 2014, Martin et al. 2017). Additionally, current dispersal patterns should have an important role on how dispersal will evolve, as demonstrated by the influence of initial sets of transfer trait values we used in this study. As a consequence, determining first the dispersive capacities of individuals within a population will be essential to studying the evolution of dispersal traits.

Furthermore, in a natural population, individuals may disperse independently of dispersal costs if an evolutionary force is driving them to disperse, for example when kin competition is too high (Cote and Clobert 2010). Modelling fixed and potentially high emigration rates such as those we implemented thus provides insights into the possible evolution of transfer traits of such a population. If transfer costs increase, many individuals may still be driven to emigrate but die while travelling, which may have strong consequences on population dynamics depending on the importance of the dispersive class of individuals on population growth rate (Caswell 1978, de Kroon et al. 1986). Thus, dispersal may become less beneficial both at the individual and population levels, and if the unbalance between costs and benefits becomes too strong, we may expect that dispersal may be counter-selected on the long term. However, all dispersal phases are interacting and their respective evolutions are intertwined (Travis et al. 2012). As a consequence, we can expect that allowing both emigration and transfer traits to evolve, and later, settlement traits, may lead to evolution of emigration probabilities towards lower values with risks, following previous studies (Travis and Dytham 1999, Bowler and Benton 2009, Awade et al. 2017), and in turn, the evolution of transfer traits towards low values might be less drastic (Travis et al. 2012). Note however that one of the conditions we modelled involved a relatively small emigration probability (0.1), which still led to reduced distance and evolved trait values. In any case, the next step will be to determine whether increased costs of transfer trigger the evolution of reduced emigration probabilities, together with higher dispersive abilities (i.e. high directional persistence and dispersal bias) compared to those we obtained in this study, consequently permitting a balance allowing for the maintenance of different dispersal tactics (for example, long-distance, short-distance dispersal and philopatry). As already suggested by several studies, studying the joint evolution of several dispersal traits, including the different phases, will shed more light into how dispersal might evolve in the future (Travis et al. 2012, Cote et al. 2017).

Dispersal evolution is highly-dependent on landscape structure, as demonstrated by many studies (Travis and Dytham 1999, Zollner and Lima 1999, Gros et al. 2006, Baguette and Van Dyck 2007,

North et al. 2011). Indeed, the distribution of suitable cells within the landscape may influence dispersal costs and thus dispersal movements (e.g. Zollner and Lima 1999). The evolution of transfer traits should also strongly depend on the amount and configuration of suitable cells in the landscape: for example, clumped habitat patches may favour individuals displaying more tortuous movements, because those have to change directions fast after dispersing to settle in a nearby cell, while in a sparse landscape, individuals may have to first travel a large distance prior to go near any other cell (see for e.g. Romero et al. 2009). Additionally, individuals may follow straighter trajectories when the percentage of suitable cells is low, because only those who travel fast to these cells may be selected, but only if transfer associated costs are not too high, in which case individuals demonstrating more tortuous movements may be favoured. Thus, the effect of the percentage of suitable habitat has to be put in relation to the transfer associated costs in order to determine its effect on dispersal traits. Similarly, we may expect that dispersal bias should increase with the decrease of suitable cells, except if transfer costs become too high. Thus, a future direction to this work should include modelling dispersal traits evolution in diverse landscape configurations.

As a conclusion, integrating dispersal costs, attraction and a more mechanistic approach of movement based on both inter-individual heterogeneity in transfer traits and a selection of displacements based on the individual perception of its surrounding environment and its trait values constituted a more comprehensive framework which helped getting more specific on the results that were already shown on the evolution of dispersal. Previous studies demonstrated that correlated movements evolved when risks increased, along with reduced dispersal distances (Zollner and Lima 1999, Hein et al. 2004, Bartoń et al. 2009), but we show that correlated movements may only occur if individuals can make the difference between suitable and unsuitable area correctly, highlighting the importance of taking into account both individual perception range and the degree of differentiation between suitable and unsuitable areas. These results also highlight that the proportion of successful dispersers may decrease with increasing risks. However, recent work has demonstrated that several dispersal tactics exist within populations (Bonte et al. 2008, Ducros et al. 2020), and we can wonder

whether some might persist better than others, for example those including increased tortuosity or reduced dispersal distances such as the progressive dispersal tactic (a movement tactic displaying an oriented but rather short and slow displacement away from the natal range, Ducros et al. 2020). It might be really interesting to implement more details into the RangeShifter software to be able to model discrete dispersal tactics and assess their respective evolutions. Thus, despite its high degree of complexity, integrating more details on the dispersal process will allow for a better understanding of eco-evolutionary mechanisms and how these may impact population dynamics.

References

Awade, M. et al. 2017. High emigration propensity and low mortality on transfer drives female-biased dispersal of *Pyriglena leucoptera* in fragmented landscapes. – *PloS one* 12: e0170493.

Backlund, P., et al. 2008. Introduction. In: *The effects of climate change on agriculture, land resources, water resources, and biodiversity*. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research. Washington, DC., USA, 362 pp.

Baguette, M., and Van Dyck, H. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. – *Landscape ecology* 22: 1117-1129.

Bartoń, K. A. et al. 2009. The evolution of an 'intelligent' dispersal strategy: biased, correlated random walks in patchy landscapes. – *Oikos* 118: 309–319.

Bartoń, K. A. et al. 2011. Risky movement increases the rate of range expansion. – *Proceedings of the Royal Society B: Biological Sciences 279:* 1194–1202.

Benton, T. G. and Bowler, D. E. 2012. Linking dispersal to spatial dynamics. – In: Clobert, J. et al. (eds), *Dispersal ecology and evolution*. – Oxford Univ. Press pp. 251–265.

Bocedi, G. et al. 2014. RangeShifter: a platform for modelling spatial eco-evolutionary dynamics and species' responses to environmental changes. – *Methods in Ecology and Evolution 5:* 388–396.

Bonte, D. and Dahirel, M. 2017. Dispersal: a central and independent trait in life history. –*Oikos* 126: 472–479.

Bonte, D. et al. 2008. Thermal conditions during juvenile development affect adult dispersal in a spider. – *Proceedings of the National Academy of Sciences* 105: 17000–17005.

Bonte, D. et al. 2012. Costs of dispersal. – *Biological Reviews 87:* 290–312.

Boulinier, T. et al. 2008. Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. – *Biology Letters 4:* 538–540.

Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – *Biological Reviews* 80: 205–225.

Bowler, D. E. and Benton, T. G. 2009. Variation in dispersal mortality and dispersal propensity among individuals: the effects of age, sex and resource availability. – *Journal of Animal Ecology* 78: 1234–1241.

Brown, G. P. et al. 2014. The straight and narrow path: the evolution of straight-line dispersal at a cane toad invasion front. – *Proceedings of the Royal Society B: Biological Sciences* 281: 20141385.

Byers, D. L. 2005. Evolution in heterogeneous environments and the potential of maintenance of genetic variation in traits of adaptive significance. – *Genetica* 123: 107–124.

Caswell, H. 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. – *Theoretical population biology* 14 : 215–230.

Cheptou, P. O. et al. 2008. Rapid evolution of seed dispersal in an urban environment in the weed Crepis sancta. – *Proceedings of the National Academy of Sciences* 105: 3796–3799.

Clobert, J. et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. – *Ecology letters* 12: 197–209.

Clobert, J. 2012. Dispersal ecology and evolution. – *Oxford University Press*.

Cornelius, C. et al. 2017. Habitat fragmentation drives inter-population variation in dispersal behavior in a Neotropical rainforest bird. – *Perspectives in Ecology and Conservation* 15: 3-9.

Cote, J. and Clobert, J. 2010. Risky dispersal: avoiding kin competition despite uncertainty. –*Ecology* 91: 1485–1493.

Cote, J. et al. 2017. Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. – *Ecography* 40: 56–73.

Dawson, T. P. et al. 2011. Beyond predictions: biodiversity conservation in a changing climate. – *Science* 332: 53–58.

de Kroon, H. et al. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. – *Ecology* 67: 1427–1431.

Delgado, M. et al. 2014. Prospecting and dispersal: their eco-evolutionary dynamics and implications for population patterns. – *Proceedings of the Royal Society B: Biological Sciences* 281: 20132851.

Denno, R. F. et al. 1996. Habitat persistence underlies intraspecific variation in the dispersal strategies of planthoppers. – *Ecological Monographs* 66: 389–408.

Ducros, D., et al. 2020. Beyond dispersal versus philopatry? Alternative behavioural tactics of juvenile roe deer in a heterogeneous landscape. – Oikos. 129: 81–92

Dytham, C. 2009. Evolved dispersal strategies at range margins. – *Proceedings of the Royal Society B: Biological Sciences* 276: 1407–1413.

Eizaguirre, C. and Baltazar-Soares, M. 2014. Evolutionary conservation—evaluating the adaptive potential of species. – *Evolutionary Applications* 7: 963–967.

Foley, J. A. et al. 2005. Global consequences of land use. – *Science* 309: 570–574.

Futuyma, D. J. 2009. Natural selection and adaptation. – In: Futuyma, D. J. (ed), *Evolution.* – Massachusetts, USA: Sinauer Associates, Inc. Sunderland pp. 279-301.

Gibbs M. et al. 2010. Organisms on the move: ecology and evolution of dispersal. – *Biology Letters* 6: 146–148.

Gogarten, J. F. et al. 2012. Seasonal mortality patterns in non-human primates: implications for variation in selection pressures across environments. – *Evolution: International Journal of Organic Evolution* 66: 3252–3266.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. – *Animal behaviour* 28: 1140-1162.

Gros, A. et al. 2006. Evolution of local adaptations in dispersal strategies. – *Oikos* 114: 544-552.

Gyllenberg, M. et al. 2002. Evolutionary suicide and evolution of dispersal in structured metapopulations. – *Journal of Mathematical Biology* 45: 79–105.

Hein, S. et al. 2004. Patch density, movement pattern, and realised dispersal distances in a patch-matrix landscape—a simulation study. – *Ecological Modelling* 174: 411–420.

Henriques-Silva, R. et al. 2015. On the evolution of dispersal via heterogeneity in spatial connectivity. – *Proceedings of the Royal Society B: Biological Sciences* 282: 20142879.

Hoffmann, A. A. et al. 2017. Revisiting adaptive potential, population size, and conservation. – *Trends in Ecology & Evolution* 32: 506–517.

Holyoak, M. et al. 2008. Trends and missing parts in the study of movement ecology. – *Proceedings of the National Academy of Sciences* 105: 19060–19065.

IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Johnson, C. A. et al. 2009. Mortality risk increases with natal dispersal distance in American martens. – *Proceedings of the Royal Society B: Biological Sciences* 276: 3361–3367.

Johst, K. et al. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. – *Oikos* 98: 263-270.

Kun, Á. and Scheuring, I. 2006. The evolution of density-dependent dispersal in a noisy spatial population model. – *Oikos* 115: 308–320.

Li, X. Y., and Kokko, H. 2019. Sex-biased dispersal: a review of the theory. – *Biological Reviews* 94: 721-736.

Martin, A. E. et al. 2017. Costs and benefits of straight versus tortuous migration paths for Prairie Rattlesnakes (*Crotalus viridis viridis*) in seminatural and human-dominated landscapes. – *Canadian journal of zoology* 95: 921–928.

Nichols, H. J. 2017. The causes and consequences of inbreeding avoidance and tolerance in cooperatively breeding vertebrates. – *Journal of Zoology* 303: 1–14.

North, A. et al. 2011. Evolutionary responses of dispersal distance to landscape structure and habitat loss. – *Evolution: International Journal of Organic Evolution* 65: 1739-1751.

Palmer, S. C. F. et al. 2011. Introducing a ‘stochastic movement simulator’ for estimating habitat connectivity. – *Methods in Ecology and Evolution* 2: 258–268.

Paranjpe, D. A. and Sharma, V. K. 2005. Evolution of temporal order in living organisms. – *Journal of Circadian Rhythms* 3: 7.

Poethke, H. J. et al. 2011. The ability of individuals to assess population density influences the evolution of emigration propensity and dispersal distance. – *Journal of Theoretical Biology* 282: 93–99.

Ponchon, A. et al. 2015. Predicting population responses to environmental change: the importance of considering informed dispersal strategies in spatially structured population models. – *Diversity and Distributions* 21: 88–100.

R Core Team. 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Romero, S. et al. (2009). Movement behavior in response to landscape structure: the role of functional grain. – *Landscape ecology* 24: 39-51.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. – *Annu. Rev. Ecol. Evol. Syst.* 38: 231-253.

Saastamoinen, M. et al. 2018. Genetics of dispersal. – *Biological Reviews* 93: 574–599.

Schluter, D. et al. 1991. Conflicting selection pressures and life history trade-offs. – *Proceedings of the Royal Society of London. Series B: Biological Sciences* 246: 11–17.

Schtickzelle, N. et al. 2006. Dispersal depression with habitat fragmentation in the bog fritillary butterfly. – *Ecology* 87: 1057–1065.

Slatkin, M. 1987. Gene flow and the geographic structure of natural populations. – *Science* 236: 787–792.

Stenseth, N. C. and Lidicker, W. Z. 1992. The study of dispersal: a conceptual guide. – In: Stenseth, N. C. et al. (eds), *Animal dispersal*. – Springer Science & Business Media pp. 5–20.

Tanaka, H. et al. 2016. Predation risk promotes delayed dispersal in the cooperatively breeding cichlid Neolamprologus obscurus. – *Animal behaviour* 117: 51-58.

Travis, J. M. J. and Dytham, C. 1999. Habitat persistence, habitat availability and the evolution of dispersal. – *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266: 723–728.

Travis, J. M. J. et al. 2010. Towards a mechanistic understanding of dispersal evolution in plants: conservation implications. – *Diversity and Distributions* 16: 690–702.

Travis, J. M. J. et al. 2012. Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. – *Methods in Ecology and Evolution* 3: 628–641.

Vitousek, P. M. et al. 1997. Human domination of Earth's ecosystems. – *Science 277:* 494–499.

Watkinson, A. R. and Gill, J. A. 2002. Climate change and dispersal. – In: Bullock, J.M. et al. (eds), *Dispersal ecology*. – Blackwell Publishing pp. 410–428.

Zollner, P. A. and Lima, S. L. 1999. Search strategies for landscape-level interpatch movements. – *Ecology* 80: 1019–1030.

Supplementary Materials

Annex I: Examples of trajectories realised with increasing directional persistence of goal bias

The two examples shown below represent how individual trajectories may vary with increasing values of directional persistence (Fig. S1) or goal bias (Fig. S2). When directional persistence increases, trajectories become straighter and individuals are less biased to deviate from their initial trajectory if they perceive a suitable cell (Fig. S1). When goal bias increases, individuals can deviate from their trajectory, but because they are biased to go away from their natal cell, they deviate from their trajectory only after having already crossed a part of the matrix to settle further from their natal area (Fig. S2).

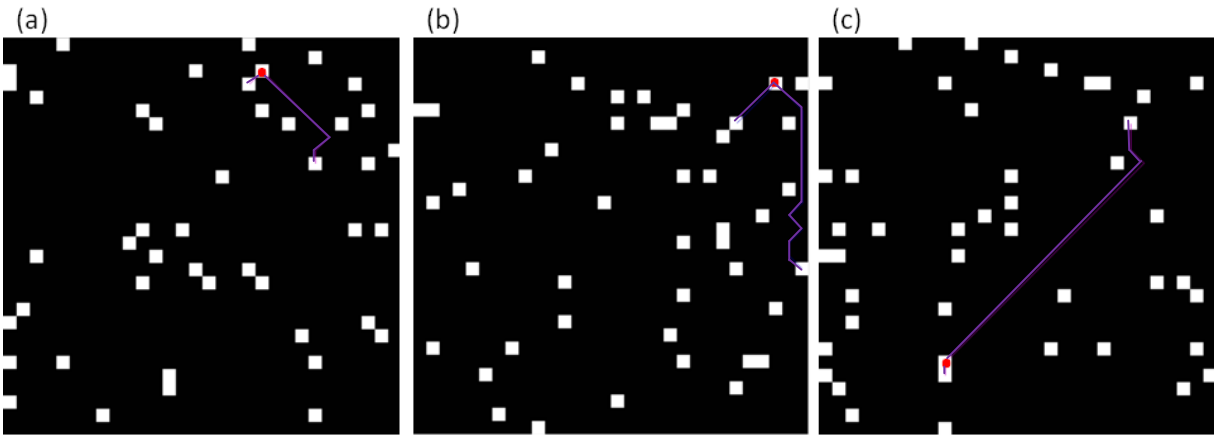


Figure S1: Examples of trajectories for three conditions of directional persistence, all other parameters being equal. (a): DP=2, (b): DP=4, (c): DP=6. White squares represent suitable cells and black squares represent inhospitable cells. Red dots represent the natal cells.

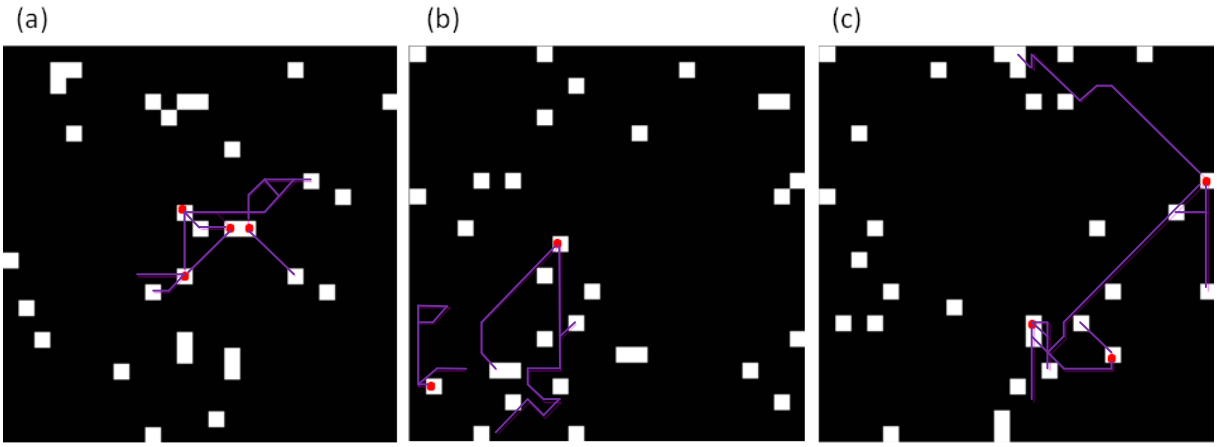


Figure S2: Examples of trajectories for three conditions of directional persistence, all other parameters being equal. (a): GB=2, (b): GB=4, (c): GB=6. White squares represent suitable cells and black squares represent inhospitable cells. Red dots represent the natal cells.

Annex II: Calculation of step-by-step movements

Initiation of dispersal: The individual is in his cell (cell X). It may move towards one of its eight neighbouring cells (blue) (Fig. S3a). The yellow area describes the area the individual perceives from its current environment. Numbers represent attraction values.

(a)

	3	2	2	2	4	6	8	
	2	1	2	2	5	3	4	
	1	7	1	2	2	2	5	
	1	8	3	X	3	2	2	
	8	5	5	3	4	7	4	
	7	6	7	6	5	4	4	
	5	4	8	9	6	5	7	

(b)

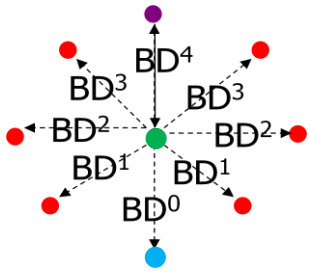


Fig. S3: (a) Example of a grid landscape containing a dispersing individual (X). Numbers indicate the attraction values for each cell. The yellow cells represent the perceptual range of the individual and the blue cell the cells in which the individual can move during its next step. The red squares indicate the cells that need to be taken into account for the calculation of the propensity to go to the targeted cell (red arrow). (b) Representation of the weights (numbers) applied to transfer traits depending on the direction an individual is taking. Here the individual came from the blue cell, arrived in the green cell, and has the possibility to go towards any of its neighbouring cell, with higher weights on cells which make it go further away from its natal cell.

For each cell in the blue area, the probability to select a given cell is equal to:

$P(\text{cell selection}) = 1/(\text{Sum}(\text{attraction values}))*1/(DP)^n*1/(GB)^n$,

With n a coefficient weighing the trait value depending on if the individual goes towards its previous direction or not (Figure S3b). For example, we can consider that the departure cell corresponds to the blue cell, and that subsequently, the individual went to the green cell. Because individuals are

expected to express directional consistency in movement, the propensity to go towards the purple cell should be higher. Thus, a high weight coefficient is applied when calculating the propensity to go towards that cell. Inversely, the weight associated to the blue cell is equal to 0. In the formula, the sum of attraction values correspond to the values contained in a square delimited around the targeted cell (red square) (Fig. S3a).

Annex III: Equilibrium strategies

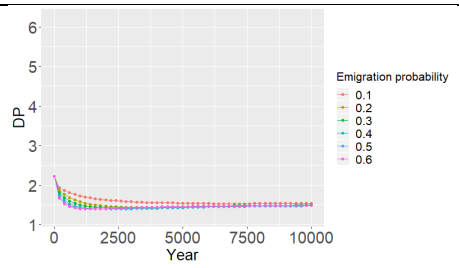
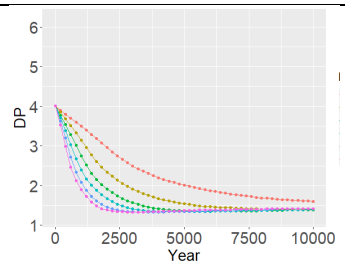
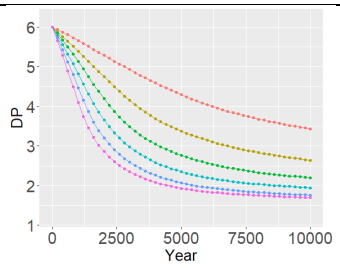
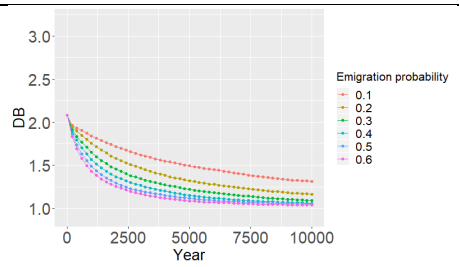
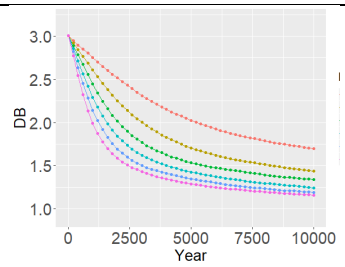
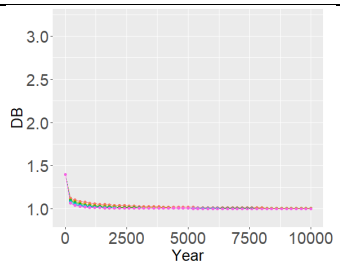
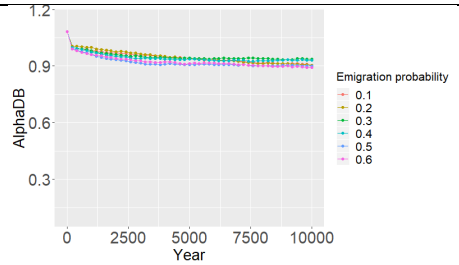
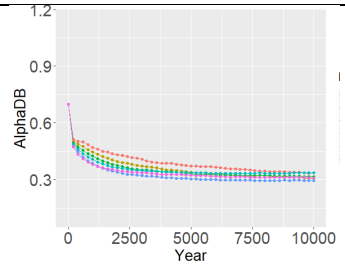
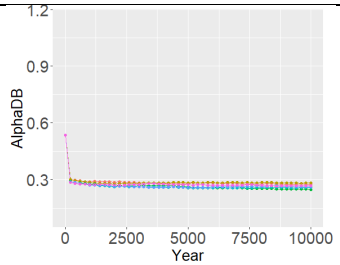
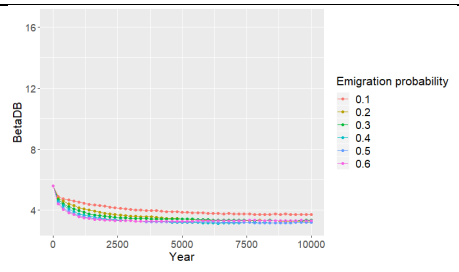
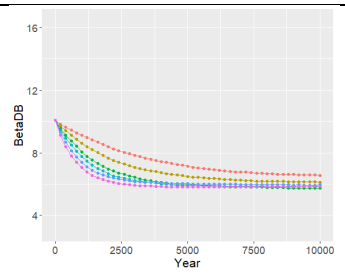
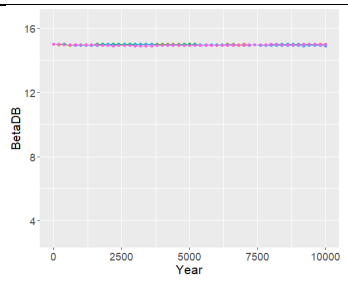
Par.	Set 1	Set 2	Set 3
(a) DP			
(b) DB			
(c) Alpha DB			
(d) Beta DB			

Fig S4: Variations in each dispersal trait (par.) (directional persistence, goal bias, AlphaDB and BetaDB) for the three sets of initial dispersal traits values, during 10 000 years for different emigration probabilities.

Annex IV: Evolution of dispersal traits with increasing mortality risk

For this analysis, we only kept the different simulation factors that were shown to explain a part of the variance for a given trait. Thus, we represented the mean variations in each dispersal trait in the last 1000 years of the simulation for these simulation factors only.

Figures 5 and 6 show the variations of directional persistence with attraction and per-step mortality or per-step-mortality and emigration probability, for sets 1 and 2 or 3 respectively. Figure 7 shows the variation of dispersal bias, in sets 1 to 3 for increasing mortality risk and emigration probability. Figure 8 and 9 show the variations in AlphaDB with increasing attraction and figure 10 and 11 show the variations in BetaDB, for varying levels of attraction and increasing per-step mortality, or varying levels of attraction only respectively.

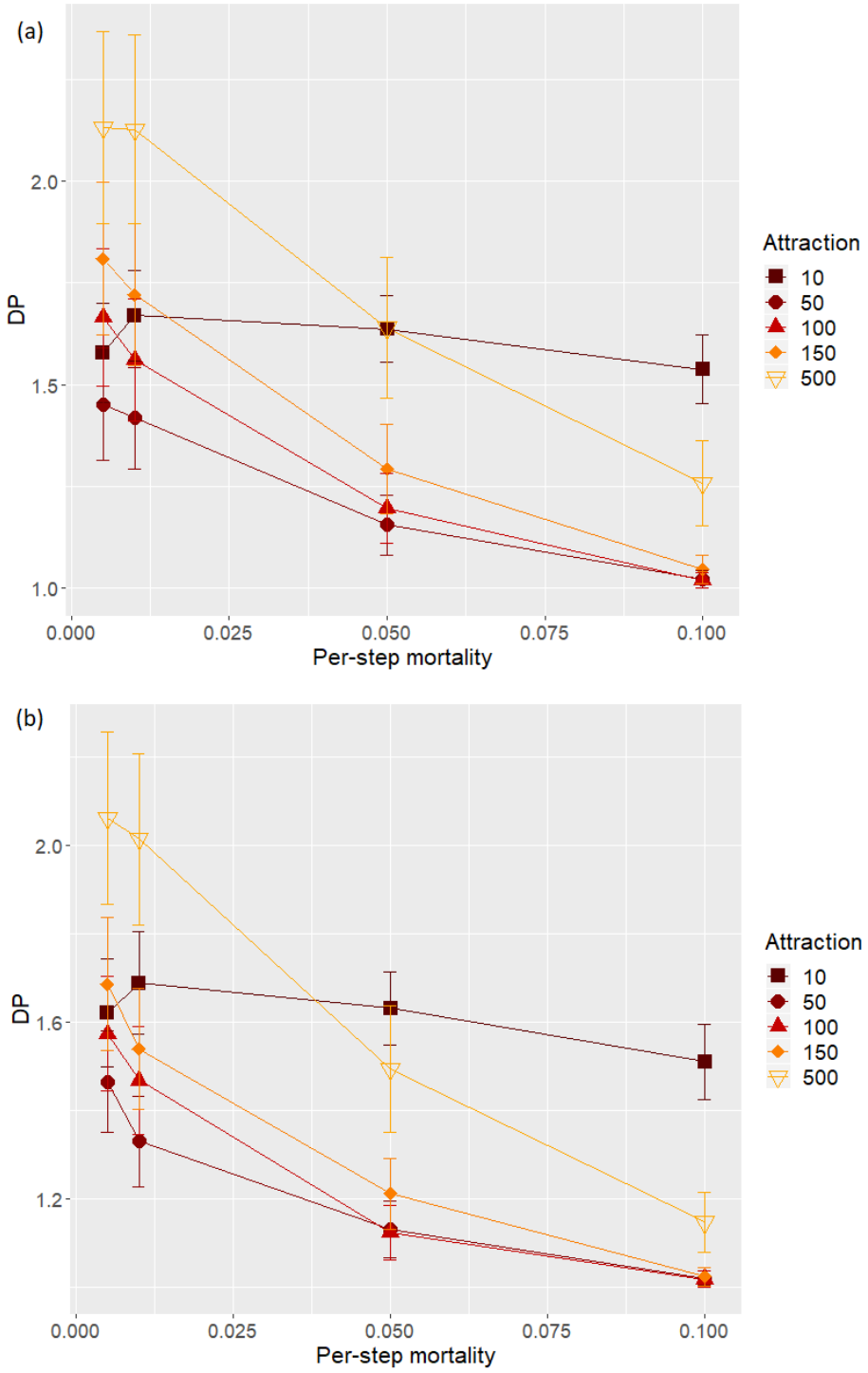


Fig. S5: Variations in mean DP averaged over the last 1000 years for increasing per-step mortality probability and varying levels of attraction. Values are given for the following simulation conditions: emigration probability = 0.1 and (a) set of initial values = set 1, and (b) set of initial values = set 2. Figure S5a. is presented in the main text but in the supplementary materials as well to ease comparisons among the different simulation conditions.

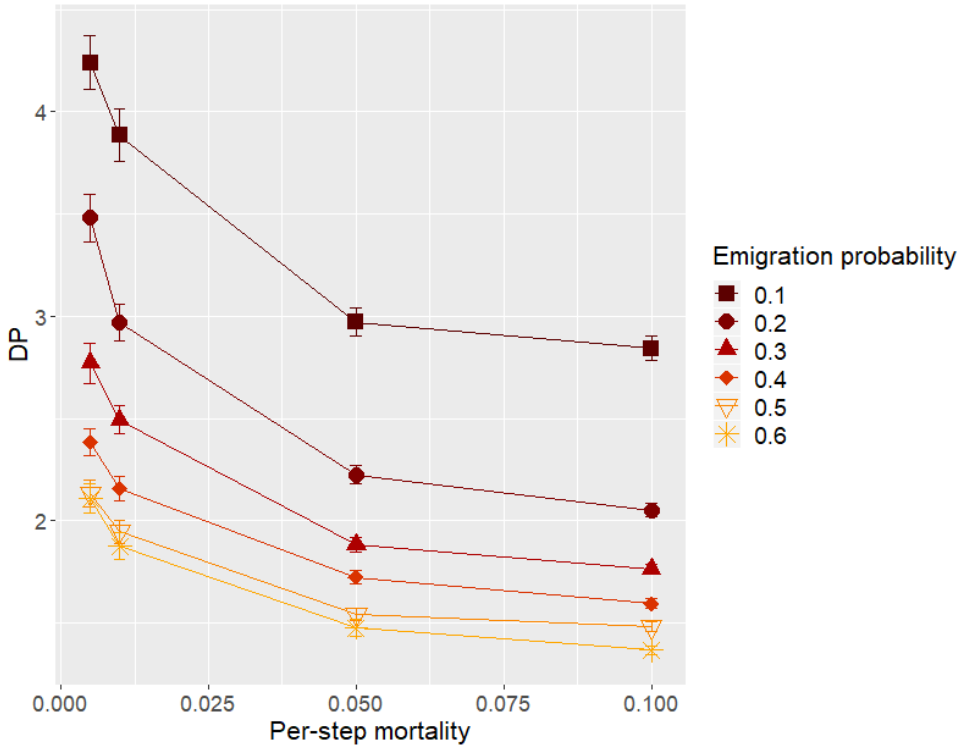


Fig. S6: Variations in mean DP averaged over the last 1000 years for increasing per-step mortality probability and varying propensity to emigrate. Values are given for the following simulation conditions: emigration probability = 0.1 and set of initial values = set 3

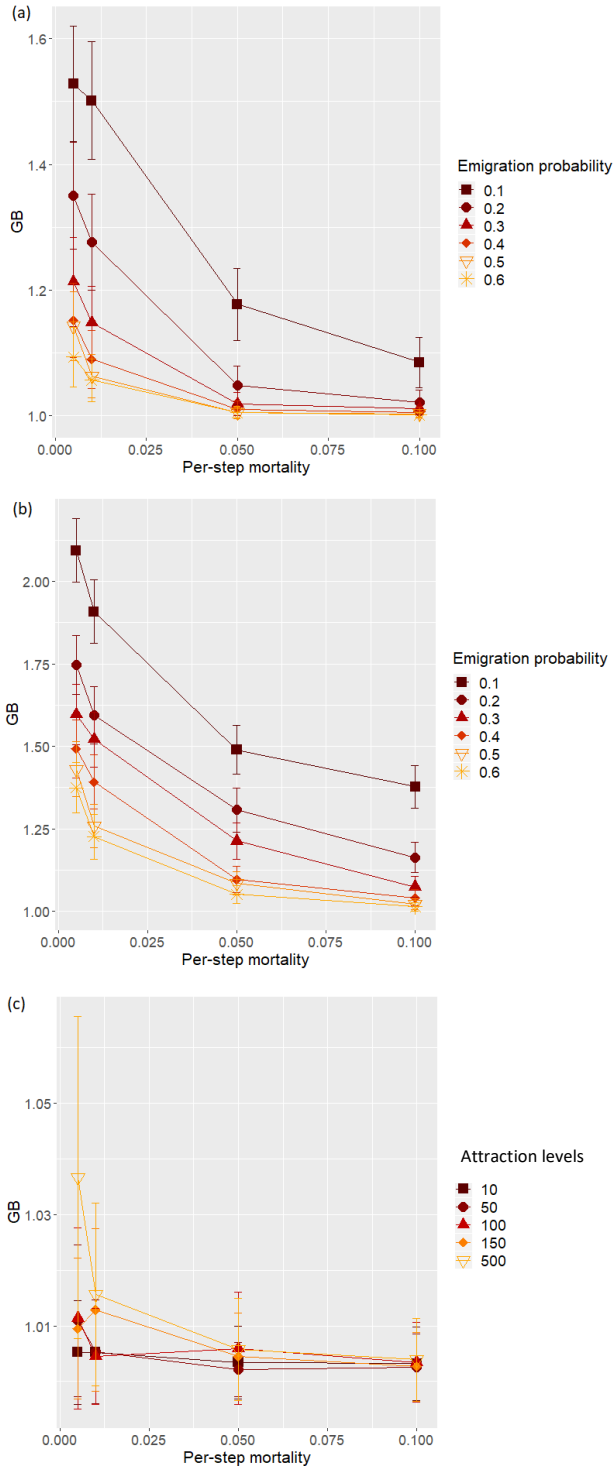


Fig. S7: Variations in mean GB averaged over the last 1000 years for increasing per-step mortality probability and varying propensity to emigrate. Values are given for the following simulation conditions: emigration probability = 0.1 and (a) set of initial values = set 1, (b) set of initial values = set 2, and (c) set of initial values = set 3

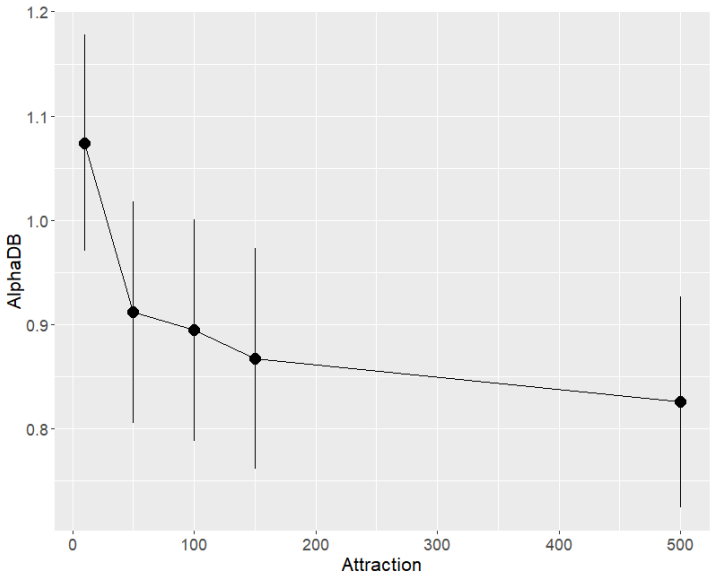


Fig. S8: Variations in mean AlphaDB averaged over the last 1000 years for increasing levels of attraction. Values are given for the following simulation conditions: emigration probability = 0.1 and set of initial values = set 1

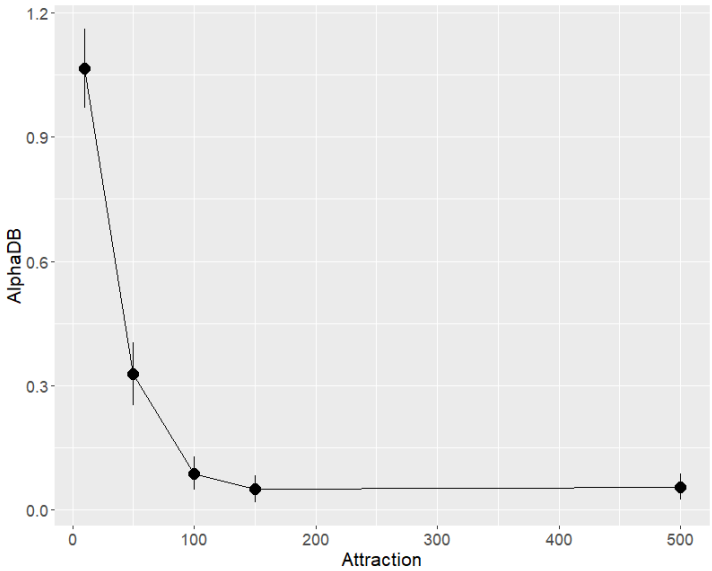


Fig. S9: Variations in mean AlphaDB averaged over the last 1000 years for increasing attraction. Values are given for the following simulation conditions: emigration probability = 0.1 and set of initial values = set 2

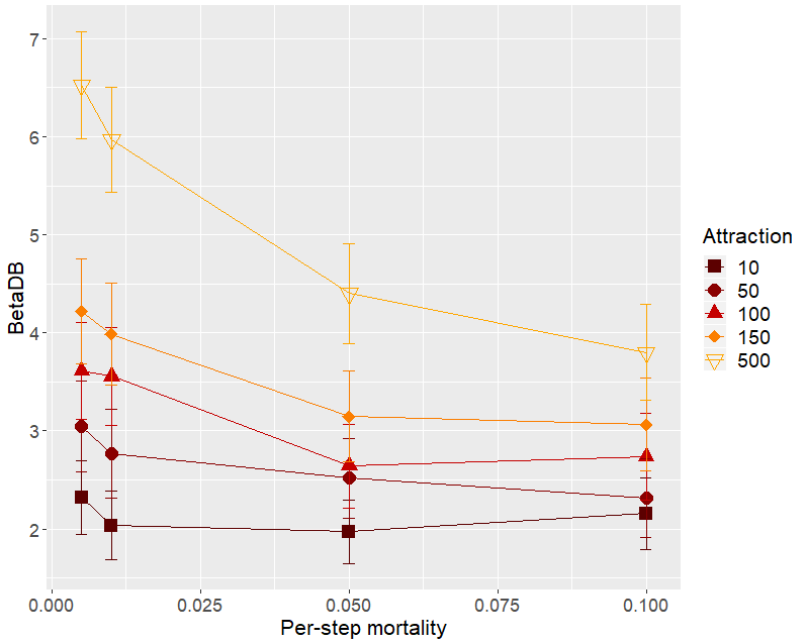


Fig. S10: Variations in mean BetaDB averaged over the last 1000 years for increasing per-step mortality probability and varying levels of attraction. Values are given for the following simulation conditions: emigration probability = 0.1 and set of initial values = set 1

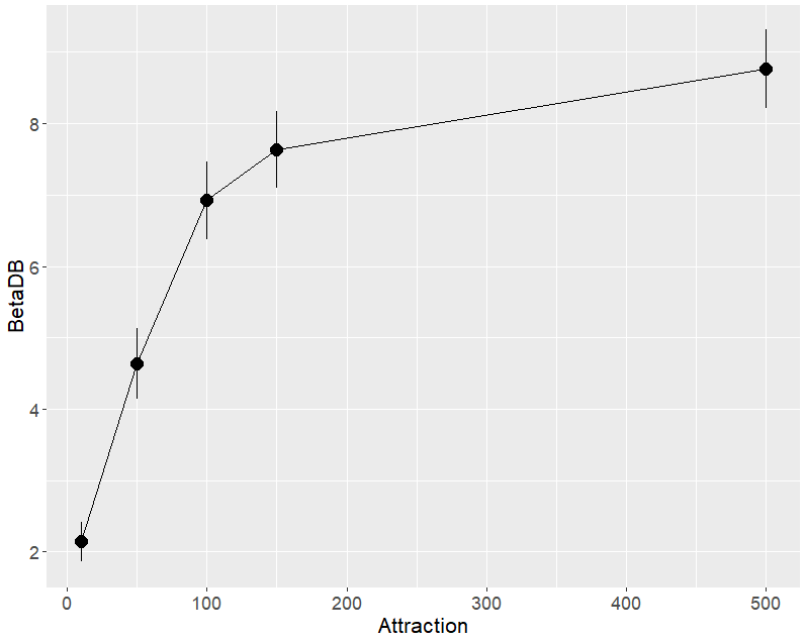


Fig. S11: Variations in mean BetaDB averaged over the last 1000 years for increasing attraction. Values are given for the following simulation conditions: emigration probability = 0.1 and set of initial values = set 2

Annex V: Number of steps dispersed after 10000 years of evolution

The number of steps travelled during dispersal decreases when per-step mortality probability increases and this effect increases with attraction.

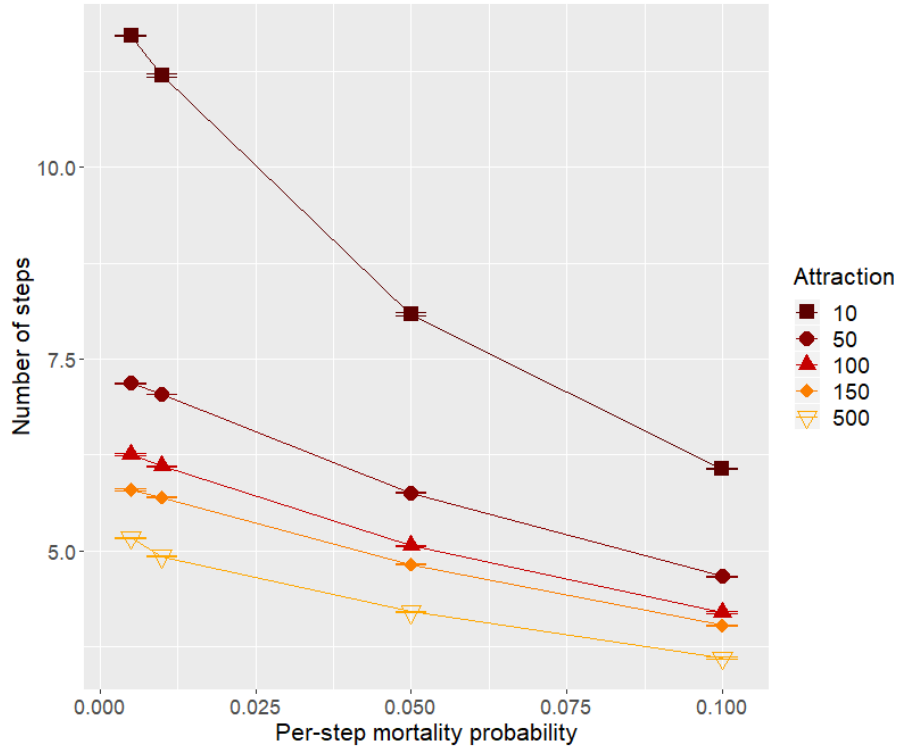


Fig. S12: Variations in the mean number of steps travelled by dispersers in the last 1000 years for increasing per-step mortality probability and varying levels of attractivity. Values are given for the following simulation conditions: emigration probability = 0.1 and set of initial values = set 1.

General discussion

In this PhD, I mainly focused on the effects of global changes on dispersal costs, and how these could affect the evolution of dispersal. I showed that some dispersal costs increase with climate change and the potential evolutionary effect of this increase in dispersal costs on dispersal. In this discussion, I will discuss these two main results and their implications for species dynamics and persistence in face of a changing world. Additionally, I also discuss the potential effects alternative dispersal tactics could have on mitigating these costs and the expected population consequences depending on the strategy adopted by an individual.

I- Global changes increase dispersal costs

1) New insights on the impacts of dispersal in a changing world

Global changes are altering many biological processes at the Earth surface, including networks of species interactions, plant production, or phenology of life-history traits (Tylianakis et al. 2008, Traill et al. 2010, Hooper et al. 2012, Alberti et al. 2017). The main objective of this PhD was to address whether or not global changes may also modify dispersal costs, in terms of survival, growth and reproduction, and how modifications in costs may translate in terms of dispersal evolution. I showed that roe deer dispersers could incur higher dispersal costs, in terms of survival, growth and reproduction, both at the medium and long term compared to philopatric individuals, and that climate deterioration may have either an additive or interactive effect on the relationship between dispersal costs and fitness components. On the other hand, roe deer did not appear to suffer from short-term costs. Indeed, I did not detect any delayed reproduction or lower growth at the age of two years old, although this type of negative costs has been shown in other species (for example in kittiwakes: Danchin and Cam 2002, Sable Island horses: Debeffe et al. 2015). Because dispersers are usually considered not to constitute a random part of the population, often being in good condition to offset dispersal costs and having a fast pace of life (Barbraud et al. 2003, Réale et al. 2010), this

first result was rather expected. However, I found both climate change and dispersal to impact survival, reproduction or growth, in an additive or interactive way and particularly at the senescent stage. While survival of dispersers was overall higher compared to the survival probability of philopatric individuals until 2002, both for adult and senescent classes, it became lower after 2002, especially for senescent individuals. Moreover, reproductive success was reduced for females when they dispersed, especially at the senescence stage and if they were heavy, and they also lost more weight at the senescent stage if they dispersed. Lastly and irrespective of dispersal status, climate change was also responsible for a lower growth in males in the last decade of the study. Thus, I mainly found effects of dispersal status and climate change on the long term (i.e. at the senescence stage). These results constitute fairly new knowledge considering not much work has been done linking global changes and dispersal costs (Cheptou et al. 2008, Duriez et al. 2009), and most studies assessed dispersal costs during emigration, transience or right after settlement (Soulsbury et al. 2008, Chaput-Bardy et al. 2010, Debeffe et al. 2015, Dingemanse et al. 2019) rather than costs at the senescent stage or throughout individuals lifetimes (but see Hansson et al. 2004, Pärn et al. 2009, Nevoux et al. 2013). Especially, substantial work has shown that fragmentation leads to an increase in dispersal-associated mortality during the transfer phase (Ferreras et al. 1992, Mennechez et al. 2004, Smith and Batzli 2006). My results are consistent with those of the few studies which have addressed more or less directly the effects of changes in environmental conditions on dispersal conditions. For example, Duriez et al. (2009) found higher mortality costs for dispersers compared to residents when habitat loss was combined with severe winters, and Germain et al. (2017) found a reduced Lifetime Reproductive Success (LRS) in dispersers compared to philopatric individuals in the context of stressful conditions. These results confirm our hypothesis that climate change may have detrimental effects on fitness, including in interaction with dispersal, which is expected to have, in turn, negative consequences on population dynamics (even though these effects mainly occurred on the long-term, and hence, are expected to have a lowered impact compared to costs that would occur on the short-term, on the juvenile or adult stage, Gaillard et al. 2000). These results add to the

recent demonstration of energetic costs of dispersal in this species, which increase when the density of roads, and thus landscape anthropization, increase (Benoît et al. 2019).

Higher demographic costs incurred by dispersers occurred simultaneously with a strong decrease in dispersal propensity. This result may be explained by a cascading effect of climate change on body mass and dispersal propensity. Because climate change leads to a reduction in body mass, and dispersal is positively correlated to body mass in many species including roe deer (Barbraud et al. 2003, Debeffe et al. 2012, David et al. 2013, Denoël et al. 2018), we can expect young roe deer might not be in sufficient condition to disperse, which could explain the observed result. Moreover, we can expect that this effect of body mass on dispersal propensity could be exacerbated by an effect of counter-selection on dispersal. Indeed, increasing costs in the context of climate change may lead to the selection of more philopatric individuals and also lead to a reduction in dispersal propensity. Theory predicts that increasing costs should counter-select dispersal if benefits simultaneously remain the same or decrease (Bonte et al. 2012, Chaine and Clobert 2012). However, not much work ever proved it empirically, and highlighted the responsibility of an increase in dispersal costs on dispersal patterns, especially in animals (but see Cheptou et al. 2008 for an example on a weed species and Duriez et al. 2009 for an example on oystercatchers). For now, many empirical and theoretical studies have shown that dispersal propensity or distance may decrease with global changes, especially if those are targeting the habitat experienced during transience, but they have not directly linked these changes in dispersal patterns to increases in dispersal costs (Bonte et al. 2003, 2007, 2008a, 2010, Schtickzelle et al. 2006, Figuerola et al. 2007, Bowler and Benton 2009, Ahlroth et al. 2010, Baines and McCauley 2018). Moreover, these studies have not highlighted which or how life history traits may be modified when environmental conditions change, and may in turn lead to the observed changes in dispersal propensity or distance. As a consequence, the demography results presented in this PhD thesis are of primary importance because they are among the first to show a direct link between an increase in dispersal costs and dispersal propensity empirically in the context of environmental change.

2) Additive or interactive effect?

While we observe an interactive effect of climate change and dispersal status on survival, the effects of these two variables seem to be only additive or single on reproduction and growth, which is contrary to our expectation. Indeed, we expected that climate change would increase the costs associated to dispersal in terms of survival, reproduction and growth. A possible explanation to this result could be viability selection, i.e. the selection of individuals which survive until they can reproduce. Indeed, in the survival analysis, I showed survival decreased with periods. As a consequence, individuals present in the dataset used for studying reproduction and growth in the last fifteen years constitute the proportion of individuals which survived in this period. Thus, I expect these individuals to be of high quality (Wilson and Nussey 2010) in the context of climate change and that they would not incur costs since they have a phenotype adapted to environmental conditions.

3) Impacts of dispersal costs on population dynamics: a matter of timing

In this PhD, I did not study the effects of the variations in demographic parameters on population dynamics. However, my results highlight the importance of considering the timing of dispersal costs, which could have important implications on population dynamics. Previous work has shown that some specific life stages can be particularly important for population growth rates, for example the juvenile stage in sturgeons, adult stage in ungulates, or one or the other depending on environmental conditions in the wild boar (Caswell 1978, Gross et al. 2002, Gaillard and Yoccoz 2003, Bieber and Ruf 2005). A decrease in the value taken by survival or reproductive values at these particular stages may thus be particularly detrimental to population growth rates. For example, the adult stage importantly contributes to population growth rate (Gaillard et al. 2000), and thus, reductions of survival at this stage may have important consequences at the population level. Thus, I expect that costs occurring at more or less long terms, including at senescence, should have different repercussions on population dynamics depending on the stage they act on. Additionally, the

phenology of dispersal, reproductive or any other life-history trait event, and their respective chronology are also particularly important to understand how global changes may impact dispersal costs. For example, individuals dispersing during the breeding stage may miss some reproductive events and incur a lowered reproductive success (e.g. baboons, Alberts and Altmann 1995). In contrast, in roe deer, dispersal is a unique process which occurs prior to any reproductive event (Gaillard et al. 1992, Debeffe et al. 2012), although some females may occasionally realise breeding excursions which allow male genome to be brought back in the females' home range (Debeffe et al. 2014), and thus, individuals may not miss a reproductive event during the dispersal period. Alternatively, some species, like the marmot, may be able to reproduce while dispersing, which will allow for gene flow to occur at multiple scales (Berger et al. 2016). Similarly, dispersal phenology may impact phenotype development, depending whether it arises prior or after growth is complete (Arendt et al. 2015). In these works, the link between global changes and their effects on potential dispersal costs was not established but we can thus expect that these costs will vary if they are attached to some specific life stages (Baines and McCauley 2018).

4) Expected effects of global changes on dispersal costs

Here I studied dispersal costs throughout the individual's life after the settlement phase, but not prior or during dispersal. However, these costs should not be taken in isolation: we also need to account for pre-emigration, emigration and transfer costs to get a full picture of the costs incurred by a disperser (Bonte et al. 2012). Because these costs are all linked to landscape structure and composition (Bonte et al. 2012), I expect that pre-emigration, emigration and transfer phases may also be impacted by global changes, and that associated costs may vary in consequence. Increasingly, studies are suggesting that global changes increase dispersal costs, although not directly measuring this increase (Schtickzelle et al. 2006, Ahlroth et al. 2010) and more work focusing on those should soon allow getting more insight on the different effects we may expect from global changes on dispersal costs. In the same study species as in this PhD, Benoît et al. (2019) showed that roe deer

energy expenditures associated to the transience phase were higher in more fragmented areas. Combining these results and future work in this population on emigration and transience costs should allow progressively determining costs incurred at the three key phases of dispersal for this species. In particular, I showed that mean juvenile body mass decreased over the last two decades, indicating individuals are in lower condition compared to previous years. Because individuals need to be in good condition to disperse and are considered to incur more costs if they are not heavy enough to disperse (Barbraud et al. 2003, Bonte et al. 2012), I expect they may incur more costs if they still disperse at a low weight. Costs may take the form of increased attrition because of the too high energy expenditures realised during transience (Benoît et al. 2019), or because they may not be able to establish a territory. This hypothesis could be tested in the Aurignac roe deer dataset for which we have detailed trajectory behaviour around the dispersal phase and information on body condition (body mass measures and physiological parameters), and since a signature of climate change has also been detected (unpublished data). Ultimately, the objective would be to link all the identified costs into a general framework to study the repercussions of global changes at the population scale, for example in terms of growth rate. Such models have rarely been developed until now (but see Anderson et al. 2009, Atkins et al. 2019), but should constitute promising research in the fields of dispersal ecology and conservation biology. This kind of framework would give us precise information on how the entire system could behave under global change and the relative implications of each demographic parameter on population growth in the context of environmental change.

5) Sex-biased dispersal

Moreover, my results show that demographic costs of dispersal and their potential variations under global change are sex-dependent. In this work, I showed that the dispersal costs incurred by males and females respectively were affected differently by climate change: males seemed to be more influenced on their survival (stronger actuarial senescence in disperser versus philopatric individuals, but only since the early 2000's) while females seemed to be more influenced on growth, as, contrary

to males, they suffered both from their dispersal status and climate change, the latter probably having an indirect effect on dispersal status through body mass. This sex-difference is rather concordant with overall literature on sex-biased dispersal commonly found in the wild (see Greenwood 1980 and Lawson-Handley and Perrin 2007 for reviews). Indeed, sex-biased dispersal may result from different costs in opposite sexes, contrasting selection pressures, or the functioning of mating systems (Perrin and Mazalov 2000, Clutton-Brock 2007, Pérez-González and Carranza 2009, Awade et al. 2017). However, this result is rather unexpected based on roe deer literature. Indeed, roe deer is considered to be a species displaying low polymorphism, and in particular, no sex-biased dispersal (Coulon et al. 2006, Gaillard et al. 2008, Debeffe et al. 2012). My work on discriminating between alternative dispersal tactics may provide an explanation to this result. Indeed, alternative dispersal strategies identified in this PhD showed a tendency to vary with sex, with females realising on average more classic dispersal events while males rather performed progressive dispersal or used the multi-range tactic. Even though both sexes ultimately moved away from their natal range, movements used within each tactic largely differed in their duration, directionality or distance. Thus, these individuals previously categorised as dispersers by previous studies actually display more complex behaviours than previously thought. Because costs and benefits are based on the actual movements realised at each stage of the dispersal process, I expect that these tactics should not incur the same costs (see more details below), which is consistent with the sex-difference observed in reproductive, survival and growth costs. Because dispersal was previously modelled as a dichotomous process in this species (ex. Coulon et al. 2006), this possible effect of alternative tactics could not be identified. I thus stress on the importance to take into account individual heterogeneity as much as possible when working on dispersal as alternative behaviours could be responsible for important changes at the demographic level. Determining whether the use of these strategies is indeed linked to variations in costs would constitute a logical and very informative next step for this species.

6) Is dispersal still playing its role?

These two main results (increased dispersal costs for dispersers at medium and late life stages, potentially linked with global change, and decreased dispersal propensity) could have strong consequences in the framework of metapopulation dynamics (Pärn et al. 2009). Metapopulations are defined as groups of individuals (i.e. populations), fluctuating in size with varying demographic parameters and linked through dispersal movements across the landscape (Hanski 1998, Clobert et al. 2004. Dispersal is at the core of metapopulations and essential for their persistence (Kokko and López-Sepulcre 2006). Movements and their effects on the persistence of populations depend on dispersal traits, landscape properties, and dispersal-associated costs (Cote et al. 2017). Because this work shows that dispersal costs may increase with global change, and that the latter also imposes costs on its own, one can question the realised effect of dispersal for metapopulations, i.e. is dispersal really accomplishing its role in metapopulation dynamics when costs increase? First, gene flow and connectivity, i.e. the degree to which the landscape facilitates movement among resource patches (Taylor et al. 1993), may both be reduced if individuals do disperse less, as the link between these metrics has been well established in the literature (Hansson 1991, Bohonak 1999, Kramer-Schadt et al. 2004, Ronce 2007, Benton and Bowler 2012, Baguette et al. 2013). Moreover, previous work has demonstrated that increased costs, including long-term cost, may decrease realized connectivity because survival and/or reproduction of dispersers decrease, and stress on the importance of considering the effects of these costs on population dynamics (Burgess et al. 2012, Cosentino et al. 2011, Edelsparre et al. 2018). A considerable decrease in dispersal propensity like the one found in this PhD may lead to significant inbreeding in dispersal-deprived populations. Moreover, dispersal is usually acknowledged for its role in population rescue or expansion to new areas (Hanski 1998, Chaine and Clobert 2012, Bonte et al. 2014). But if dispersal is followed by a decrease in reproductive success or survival, dispersers may not fulfill their role as founders of a new population, or not as well as they would have without these costs. Again, this potential outcome

depends on the actual impact of each demographic age class on demographic rates (Saether and Bakke 2000, Gaillard et al. 2000, Sim et al. 2011).

Thus, dispersers incur a whole range of dispersal costs which are expected to be modified by current global changes, and with potentially far-reaching consequences for population dynamics. Because dispersal is a highly-heterogeneous process, we may expect that if individuals adopt alternative dispersal strategies to disperse, they may not incur the same costs.

II – Alternative dispersal tactics: do they suffer the same costs?

1) Why dispersal tactics matter?

Previous empirical and modelling work largely showed that movement properties (related to individual behaviours during dispersal and including for example emigration probability, directionality, dispersal distance, etc.) led to different costs or benefits to a species, in link with the environmental characteristics (for a review: Bowler and Benton 2005; for empirical studies: Trakhtenbrot et al. 2005, Smith and Batzli 2006, Johnson et al. 2009, Debeffe et al. 2012, Awade et al. 2017, Addis et al. 2019, Sawyer et al. 2019; for modelling studies: Stamps et al. 2005, Barton et al. 2012). As I previously mentioned, integrating individual heterogeneity in movement is fundamental for better understanding the effects of dispersal costs on population dynamics. The importance of the inclusion of individual heterogeneity has been strongly highlighted in recent research (Hawkes 2009, Clobert et al. 2009, 2012, Bestion et al. 2015, Brown and Crone 2016), but for now, is still rarely accounted for in research articles about dispersal, in particular in the form of alternative dispersal tactics, i.e. the set of alternative behaviours an individual may potentially express in response to a given environmental context (but see Bonte et al. 2008a, Hogan and al. 2014 for two examples). However, the consideration of the variability of dispersal tactics would provide a more

comprehensive view of the process. First, tactics are integrative in the sense that they take into account all single movements the individual realized (depending on the precision of GPS data; more GPS points recorded allow for a better estimation of movement paths). The expression of tactics results from successive movement decisions and as such, considering the totality of these movement decisions gives more insight into the dispersal patterns compared to working only one aspect of dispersal patterns, for example, distance or emigration propensity. Moreover, the three phases of dispersal and their associated costs interact, thus, considering the whole process will allow taking into account these interactions between phases (Travis et al. 2012). Additionally, because selection can act on each dispersal trait, and affect them differently, working on one phase independently of each other may provide a biased or incomplete vision of how dispersal may be impacted by changes (Awade et al. 2017). Thus, the only way to really grasp the overall impact of dispersal costs on realized dispersal is to work on tactics. Considering a dispersal tactic will allow accounting for both time and space properties of successive movements at the same time, and analysing the entire process and the underlying mechanisms explaining the dispersal patterns we observe (Bonte et al. 2008b).

2) Two main implications of alternative tactics in a changing world

a. Varying costs for varying tactics

In this manuscript, I identified six discrete dispersal tactics which individuals exhibit depending on environmental properties they experience and based on their phenotype. The identification of these tactics should have two main implications in the context of global changes. First, individuals should not incur the same costs depending on the strategy they use, and these costs may vary with environmental degradation. Indeed, substantial work has shown that variations in environmental properties may affect individuals differently depending on their dispersal movement characteristics

or ontogeny (Massot et al. 2002, Bestion et al. 2015, Cote et al. 2017). For example, dispersal costs have been shown to increase with increasing distance in several species (Smith and Batzli 2006, Johnson et al. 2009, Awade et al. 2017). Because the dispersal tactics I identified are in part characterised by different dispersal distances, I may expect that they would also imply different risk costs. Moreover, habitat fragmentation or destruction often lead to higher risks to individuals crossing the landscape (Bonte et al. 2012), thus, I expect that individuals adopting long-distance or long duration dispersal tactics, such as classic dispersal or pseudo-dispersal, in the context of fragmentation should incur higher risk costs compared to individuals moving smaller distances or during shorter periods of time (Cote et al. 2017, Atkins et al. 2019). On the contrary, repeated stopovers through the landscape, as detected in several of the identified tactics (multi-range tactic or for some classic dispersers) may have a similar role as stepping stones. Stepping-stones consist in any landscape element that an individual may use to alt prior to continue its displacement towards a suitable patch (Simberloff et al. 1992) and can prove useful for increasing dispersal success, especially in fragmented habitats (Mandujano et al. 2004, Kramer-Schadt et al. 2011, Saura et al. 2014, Yang et al. 2016). Individuals using these tactics may be able to track resources and stop if travelling through the unsuitable habitat is too costly. I expect that these kind of tactics could be extremely valuable if environments become too harsh for an individual to cross it at once. However, increasing the amount of stopovers may also be detrimental for individuals if other risks are present during the transient phase (for example, mortality risks by predation or trapping) and they might incur a lower dispersal success. Thus, the interaction of several behaviours leading to costs or benefits to their users into a single tactic may lead to different costs, which remains to be verified in future works. In conclusion, I expect a given tactic to be more or less suitable depending on the environment and its modifications.

b. *Alternative tactics may help some individuals coping better with environmental changes*

As a consequence of these varying costs, populations displaying a large heterogeneity in the expression of individual dispersal tactics should be able to respond better to the environmental factors creating these costs. Indeed, the high degree of plasticity individuals can display in dispersal tactics may be very beneficial to mitigate dispersal costs depending on the environmental conditions they are experiencing, as has already been suggested by several authors, including Bowler and Benton (2005), Clobert et al. (2009), Bonte et al. (2012). One particularly relevant example of how plasticity in dispersal may help mitigating dispersal costs in face of climate change is provided by *Erigone* spiders, which adopt either rappelling or ballooning depending on environmental conditions they experience (Bonte et al. 2008a). Individuals register the temperature they incurred during development to project on the environmental conditions they are likely to experience once adults. Indeed, the proportion of suitable habitat is related to the temperature experienced during the previous season. Then, this information influences individual dispersal strategy. However, despite their fundamental role in response to global changes, discrete alternative tactics have not yet been thoroughly investigated under global change. In my chapter on dispersal heterogeneity, I showed that some tactics were preferred according to the environmental conditions incurred in the natal range. In particular, individuals born in more disturbed areas were more likely to classically disperse. We could make the hypothesis that these tactics may arise in different environments because the latter trigger varying costs to the respective users of these tactics. For example, a long-distance movement requires a good body condition (Barbraud et al. 2003, Bonte et al. 2012), and thus classic dispersal tactic may be more selected for individuals born in high-quality habitats. In the context of environmental change, I expect that some tactics may be preferentially expressed if they confer advantages to individuals selecting these tactics. For example, when risk costs increase, individuals displaying straighter and shorter movement paths may have a higher dispersal success, especially if they have a good vision of their environment and perceive a suitable area to reach (Zollner and Lima

1999, Schtickzelle et al. 2006, Biz et al. 2017). This way, individuals spend less time in the unsuitable habitat and reduce the associated costs of transfer (Atkins et al. 2019). The results I obtained in the fourth chapter of this PhD, by modelling the evolution of dispersal with increasing mortality costs associated to the transfer phase, also support this hypothesis. I found that individuals realising the shortest movement paths (Euclidian distance), by increasing the tortuosity of their trajectory and reducing their bias to go away from their natal cell at each step, survived better. In turn, selection favoured these individuals, and thus some tactics, on the long term. Another way to mitigate an increase in dispersal costs with global change could be to modify movement directionality, which was shown to vary in the alternative tactics I identified. Progressive dispersers followed a continuously oriented movement towards a particular direction, while individuals adopting the multi-range tactic changed movement orientation frequently. Cosentino et al. (2011) showed that the tiger salamander (*Ambystoma tigrinum*) is able to orientate its dispersal movements towards suitable habitats and strengthen its directionality when desiccation risks within its environment increase. I thus expect that if habitats change in a way that structures resources in space, with clearly unsuitable and clearly suitable habitats for roe deer, and that the latter can perceive this difference, we may witness more orientated dispersal events such as progressive dispersal or classic dispersal. That is also something I obtained in my fourth chapter, as individuals which could better discriminate between suitable and unsuitable habitat maintained a higher directional persistence compared to individuals dispersing in landscapes in which the contrast between suitable and unsuitable habitats was less clear. Alternately, if resource locations are highly variable, individuals may have to change ranges frequently and use the multi-range tactic (Couriot et al. 2018). Additionally, the use of refuge areas, such as corridors or stepping stones, may help mitigate dispersal costs, because these provide a shelter for individuals dispersing and may favour movement between ranges (Simberloff et al. 1992, Aars and Ims 1999, Mech and Hallett 2001, Castellón and Sieving 2006). It would be really interesting in a second step to determine whether some tactics are leading to a more frequent use of some particular landscape elements, such as refuge zones or open areas, which are risky but highly

nutritive for roe deer (Hewison et al. 2009). Dispersers may also modify their dispersal propensity based on meteorological or natal habitat conditions, as has been shown for different species (for example, wind velocity and maternal patch size: Bonte et al. 2007, disturbance in the natal habitat: Entling et al. 2011, the combination of habitat fragmentation and temperatures: Delattre et al. 2013).

More globally, species may exhibit many different behaviours indirectly linked to the dispersal movement itself and allowing them to adjust their dispersal tactic to environmental changes. In this PhD thesis, I characterized alternative tactics differing in spatial movement timing, directionality and duration, but tactics may differ by other factors which could allow species to adapt. Because costs associated to dispersal may not be the same in different ecosystems (Baguette et al. 2013), changing dispersal medium may provide new possibilities for a species which is capable of moving through different types of landscapes but is limited in using one of these mediums (for example, *Erigone* spiders may disperse both in air or on mainland: Bonte et al. 2008a, amphibian species may disperse both in dry or flooded habitats, Fortuna et al. 2006). Individuals may also benefit from gathering information from individuals prior and during their movements through the landscape, i.e. perform informed dispersal (Clobert et al. 2009). This could for example take the form of explorations of their surroundings before dispersal (Roper et al. 2003, Cox and Kesler 2012, Debeffe et al. 2012), which could mitigate dispersal costs incurred by individuals. Indeed, explorers may for example gain information on the reproductive potential of an area prior to settling there (Dittmann et al. 2005, Ward 2005, Boulinier et al. 2008, Ponchon et al. 2015a, 2015b), or gain familiarity with it which alleviates costs (Yoder et al. 2004, Haughland and Larsen 2004, Cox and Kesler 2012). Individuals may also gather information from immigrants (Cote and Clobert 2010). Thus, individuals realising informed dispersal should be better able to determine the advantage or inconvenient of moving towards a particular habitat, and may suffer less costs when environments change, except if the acquisition of information itself becomes too costly (Delgado et al. 2014). Finally, for species where dispersal is not fixed to a particular life stage, we may expect individuals to adjust the proportion of temporal or spatial dispersal they may realise. Patterns of expression of these two types of tactics

appear to be complex (Den Boer 1968, Buoro and Carlson 2014), but I expect that individuals may for example disperse at a time of the year which minimizes risks (Ekernas and Cords 2007), or if they can use both natal and adult dispersal, that they may preferentially use one or a combination of both, depending on which minimizes more the risks, which may have different repercussions on populations (see a example on kittiwakes, Ponchon et al. 2015a).

Thus, adopting alternative dispersal tactics could result in different costs and thus different life histories. Since dispersal is determined by the balance between costs and benefits, I expect that increasing costs due to environmental deterioration may gradually have repercussions on the evolution of dispersal, as suggested by several authors (Bonte et al. 2010, Baguette et al. 2013, Travis et al. 2013, Cheptou et al. 2017). More precisely, some dispersal tactics might be privileged over others, and thus, individuals may gradually evolve to some specific strategies more adapted to global changes (Bonte et al. 2008a, Teller et al. 2015). However, all individuals do not respond the same way to environmental pressures (Baguette et al. 2013, Cote et al. 2017), and as for now, we do not have a clear idea of how dispersal may evolve with global change and increasing associated dispersal costs. My PhD thesis aimed to shed more light on this question, through the study of the evolution of dispersal traits.

II- Dispersal evolution with increasing dispersal costs

Dispersal has a genetic component, and is determined by one or multiple potentially heritable traits depending on the species considered (Doligez et al. 2009, Saastamoinen et al. 2018). As such, modelling dispersal evolution needs to take into account this genetic origin of dispersal. Until now, few studies explicitly modelled dispersal traits (i.e. specific genes containing one or several loci and whose variation may be transmitted to the next generations) when they studied dispersal evolution, i.e. they did not fully model the genetic component linked to the biological notion of traits (but see Bonte and al. 2010 and Henriques-Silva et al. 2015). Rather, they used probability functions from

which movement parameter values were drawn, and the latter were then transmitted to the next generation with a mutation probability, but without explicitly modelling the diversity of loci (for example, Zollner and Lima 1999, Bartoń et al. 2009). This is especially true when modelling the three phases of dispersal: no study to my knowledge explicitly studied the joint evolution of the three phases of dispersal by the use of dispersal traits, although many studies advocate taking into account individual variability in traits and study the joint evolution of these traits (Clobert et al. 2009, Travis et al. 2012, Burgess et al. 2015, Bestion et al. 2015, Saastamoinen et al. 2018). In this PhD, I moved one step forward by modelling the evolution of dispersal traits associated to the transfer phase for different emigration probabilities.

1) Consequences on population dynamics

In this PhD, I showed that when mortality costs increase during the transfer phase, movement autocorrelation, and dispersal bias, distances and success may decrease. As explained in chapter IV, these results may have many implications for species dynamics, including on a decrease in connectivity, gene flow, carrying capacity, competition, population ranges and in the potential for population rescue (Hansson 1991, Bohonak 1999, Kramer-Schadt et al. 2004, Ronce 2007, Benton and Bowler 2012, Bonte et al. 2012, Baguette et al. 2013). Moreover, natural systems are complex and dispersal incurs a wide variety of costs which are susceptible to vary with global change (Bonte et al. 2012), thus, I expect that several costs should influence dispersal evolution simultaneously, and thus impact population dynamics jointly. Moreover, I also showed in this PhD that three main fitness components (survival, growth and reproduction) may be negatively impacted by climate change, although these effects mainly occurred at the long-term, which may have lower impacts on population dynamics than short-term effects, i.e. at juvenile or adult stages (Gaillard et al. 2000), which I am going to discuss thereafter in link with my results on dispersal evolution modelling. I expect that the fitness of individuals will not be impacted in the same way if individuals only incur mortality costs during transience or if they both incur mortality during transience and other long-

term costs, such as reproductive or attrition costs from the influence of several environmental factors.

- Population rescue

An increased mortality or decreased reproduction for dispersers reduces their performance when they settle in a new area, and thus, should limit their role in population rescue. As a consequence, population rescue should be limited both by a decreased in the number of individuals successfully dispersing (because of transfer-associated mortality), and a decreased fitness after dispersal. In turn, if population rescue becomes limited, risks of extinction for some populations increase, and as a consequence, the viability of metapopulations may decrease.

- Gene flow

Gene flow should be largely impacted by the way dispersal evolves, and at different levels. Because dispersal tends to evolve towards rather short-distance movement paths, gene flow might be reduced (Coulon et al. 2004). Additionally, since dispersers tend to incur medium to long-term costs in terms of demography, and have a poorer fitness when they settle compared to philopatric individuals, they may not transmit their genome to the next generation as well as they should have without these increased costs, which will also limit gene flow. A study from Hansson et al. (2004) highlighted that short and long-distance dispersers may not incur the same dispersal costs, and that in consequence, gene flow is decreased for long-distance dispersers which incur more costs. Lastly, global changes have been shown to decrease individual propensity to disperse in this study but also in other study systems in the literature (Bonte et al. 2003, 2006, 2008a, 2010, Schtickzelle et al. 2006, Figuerola et al. 2007, Bowler and Benton 2009, Ahlroth et al. 2010, Baines and McCauley 2018), which also means decreased gene flow. This may have strongly detrimental effects on populations as decreases in gene flow elevate extinction risks (Spielman et al. 2004). Global change may thus have consequences at different levels on dispersal, including many I did not investigate in this PhD, for example pre-dispersal energetic costs, which should all, in turn, have consequences on population

dynamics and should have repercussions on the species potential to persist in a changing world (Berg et al. 2010, Bonte et al. 2012). Both the effects on gene flow and connectivity will also be strongly impacted by the proportion of individuals successfully dispersing, which may decrease when mortality risks increase.

- Communities

Finally, I expect that the repercussions of dispersal evolution on population dynamics in a context of environmental change are going to affect species but also communities. Indeed, species are linked together with all sorts of interactions such as mutualism, predation, etc. Thus, if the functioning of one species is modified, we can expect communities to be modified as well, and all the system to change (Ferriere et al. 2000, Parmesan 2006, Berg et al. 2010). In particular, in the case of seed dispersal by animals, the plant species depends on the animal species for its dispersal. Thus any event preventing the animal dispersal may in turn prevent seed dispersal. For example, hunting may have strong impacts on species interactions and maintenance if the dispersal movement of a plant species is impaired by the killing of animal dispersers (Wang et al. 2007, Brodie et al. 2009). It is the case of a tree species, *Choerospondias axillaris*, whose seeds are dispersed by mammals in Thailand (Brodie et al. 2009). However, poaching is responsible for a decrease in dispersal of these mammals, and thus, seed dispersal is reduced, leading to a lower growth rate in the tree population. I did not study such community interactions within my PhD thesis but this would constitute a very interesting research avenue once the dispersal patterns of some populations and their evolution will be well described and comprehended.

2) What about dispersal syndromes?

Dispersal syndromes are widespread in the wild and consist in covariation between dispersal-associated traits and other life-history traits (Sih et al. 2004, Ronce and Clobert 2012). These syndromes have been demonstrated in a wide range of species, especially terrestrial ones (Burgess et

al. 2015), may happen at any stage prior, during or after the dispersal process, and may be related to any of the three phases of dispersal (Cote et al. 2017). Dispersal syndromes may arise for three main reasons: (1) they can confer an advantage to dispersers, which allows them to increase their dispersal success, (2) because dispersal as well as other biological processes may be costly, trade-off will limit the expression of certain phenotypes if the individual disperses and (3) when some traits confer an advantage to dispersers, even if this does not increase dispersal success itself (Clobert et al. 2009). Traits forming a dispersal syndrome may include morphological, physiological and behavioural characteristics (Clobert et al. 2009). Personality traits, such as exploratory behaviour, submissive behaviour, or neophobia, have been shown to be correlated with dispersal traits, such as activity, dispersal propensity, distance or timing as part of a dispersal syndrome in several species (Fraser et al. 2001, Dingemanse et al. 2003 in great tits, Sarno et al. 2003 in guanacos, Cote and Clobert 2007 in the common lizard, Cote et al. 2011 in the mosquitofish, Debeffe et al. 2014 in roe deer, Cooper et al. 2017 in red squirrels, Coates et al. 2019 in carp gudgeons; see Cote et al. 2010 for a review). Dispersal syndromes have also been identified with phenotypic traits, such as body mass, life-history traits, such as survival (Stevens et al. 2014, Denoël et al. 2018), or other traits linked to mating strategies (Massol and Cheptou 2010) or to the concentration in hormones, for example, corticosterone (Silverin 1997). It is important to note that the interaction of dispersal traits with these traits varies greatly both between and within species (Ronce and Clobert 2012, see Stevens et al. 2014 for a review).

In a context where dispersal traits may be altered by global change, I expect that dispersal syndromes should be modified and that traits correlated to dispersal traits may evolve following the evolution of the latter. This expectation has already been formulated by Cote et al. (2010), who stated that dispersal syndromes are expected to vary with ecological or social contexts, and from other authors who mentioned that the evolution of dispersal traits should also lead to modifications in traits correlated to dispersal (Clobert et al. 2009, Cote et al. 2017). Much work is yet necessary to explore how these traits may exactly evolve with dispersal evolution, which may represent a

particular challenge considering the high variation in dispersal syndromes (Ronce and Clobert 2012, Cote et al. 2017), although current scientific literature should help orienting our discussion. In particular, there are three ways in which dispersal syndromes may be modified: they could be created, disappear or the interaction between traits could be altered. First, dispersal syndromes could emerge because of global change (Cote et al. 2017). For example, if dispersal propensity is reduced because the environment surrounding habitats is too risky, we can expect density to increase and potential variations in agonistic behaviours (Fleming and Johansen 1984, Brown et al. 1992, Sakakura et al. 1998, Wildy et al. 2001). Because low dispersal propensity can be associated to high sociality or cooperative behaviours in some species or populations (Arnold 1990, Purcell et al. 2012), it would be interesting to test if behaviours such as a higher sociality or more cooperative behaviours may evolve in these systems as dispersal evolves towards lower propensities to emigrate. Secondly, dispersal syndromes may be suppressed. For example, dispersal has been associated to mobility, exploration and activity in roe deer (Debeffe et al. 2014). I expect that if costs such as fragmentation increase, tactics such as the classic dispersal tactic may incur more costs, because individuals usually disperse for long-distances, and that distance is associated to higher risks in fragmented habitats. As a consequence, selection should favour individuals adopting other tactics, such as the progressive dispersal or multi-range tactic, and thus, I expect that energy expenditures associated to growth or mobility may not be as necessary and the selection for corresponding traits could be reduced. Similarly, if individuals disperse less far, we can expect their tendency to explore far away from their natal habitat may also decrease. Lastly, dispersal evolution may not necessarily create or suppress previously existing dispersal syndromes, but may adjust the way several traits are correlated (Cote et al. 2017). Dispersal syndromes are both species and context-dependent, and thus, I expect the evolution of dispersal syndromes with global changes to lead to a high variability within and between habitats.

The evolution of traits correlated with dispersal may also have great implications in terms of population dynamics and persistence, and it is fundamental to determine to which extent they might

be modified, especially for endangered species. Indeed, because of the actual expression of dispersal syndromes, some species may incur both additional dispersal costs when the environment deteriorates, and negative consequences associated with traits comprised in the syndrome (Dahirel et al. 2015). For example, in snails, high specialization and low dispersal ability are genetically related, and thus, when habitat is fragmented, specialists may face both costs in terms of lower dispersal success and higher vulnerability to fragmentation because of specialization (Dahirel et al. 2015). Moreover, if dispersal syndromes evolve, as suggested by the literature (Duputié and Massol 2013, Atkins et al. 2019), I expect that some may lead to additional negative costs to dispersers. For example, if dispersers are suffering from habitat deterioration and incurring more costs associated with dispersal, dispersal should evolve towards fewer individuals dispersing, or less far and thus, the role of dispersal should be reduced and impact population dynamics (in terms of gene flow, population rescue etc. Ronce 2007). But if in addition, the decrease in dispersal efficiency is associated with a modification in other traits linked to dispersal, for example traits related to habitat selection or mating systems (Sinervo et al. 2006, Cheptou and Massol 2009, Massol and Cheptou 2010), dispersers may suffer from additional costs because of their syndrome. For example, in the aforementioned example on snails (Dahirel et al. 2015), we may expect that if habitat fragmentation leads to higher mortality in dispersing individuals, the population may evolve towards less or shorter dispersal events, and thus lower dispersal abilities. Because of the association of specialization and low dispersal abilities in a syndrome, this may lead in turn to an evolution towards high specialization, and more vulnerability in face of global changes because a large part of the population could exhibit these two characteristics. Thus, the existence of dispersal syndromes may lead to additional costs, directly or indirectly linked to dispersal itself, whereby individuals could incur a double penalty from dispersing, which would in turn impact population dynamics.

Alternatively, selection may also act on traits associated with dispersal through the dispersal syndrome to reduce dispersal costs (Cote and Clobert 2010). For example, we may expect that if

predators increase, due to species invasion or increased poaching for example, then individuals may develop anti-predator strategies (Cote et al. 2017, Atkins et al. 2019). Because dispersers possessing these anti-predator strategies may survive, contrary to dispersers who do not possess these strategies, selection may favour the emergence of dispersers with anti-predator behaviours, potentially leading to the emergence of a syndrome which reduced new dispersal associated costs. Individuals may also develop behaviours which could enhance their dispersal success, for example more aggressive behaviours (Duckworth and Badyaev 2007, Cote and Clobert 2010).

3) Interplay of numerous ecological factors and selection pressures

Evolution is subjected to several biotic and abiotic factors, some of which we highlight in this PhD, and others I did not study. Because the modelling of dispersal evolution is highly theoretical, results need to be adjusted with the biological reality of the species which is studied. This section aims to provide a general overview of the many factors that could impact dispersal evolution, including in a context of environmental change, and that need to be considered when one wants to model dispersal evolution. These are of two main types: species biology and environmental characteristics.

a. Species biology

(i) Adaptive potential

Species are characterised by an adaptive potential, i.e. the "ability of a species or a population to respond to selection by means of phenotypic or molecular changes" (Eizaguirre and Baltazar-Soares 2014). Adaptive potential may allow species to persist in their usual range if they can cope with environmental changes (Berg et al. 2010). Alternatively, if this potential does not fit with the latter, it can lead individuals to use dispersal as a way to cope with global change. As a consequence, if individuals can adapt without moving, I expect dispersal will not be under strong selection for individuals to survive and reproduce, and thus, there may be low selection pressure on the corresponding dispersal traits. Thus, the evolution of dispersal first depends on the adaptive potential of a species.

(ii) Dispersal tactic

- Dispersal capacity

Secondly, if individuals disperse, their dispersal capacity and the tactic they use during dispersal should also have strong impacts on dispersal evolution. Indeed, some categories of individuals may be more or less efficient at dispersal. For example, habitat specialists usually have poorly developed dispersal behaviour and thus, dispersal is more selected by generalists compared to specialists when risks increase (Bonte et al. 2003, 2009, Tischendorf et al. 2003, Dahirel et al. 2015). For example, in European land snails, specialists exhibit poorly developed dispersal structures and realise slower or more tortuous trajectories (Dahirel et al. 2015). Because I showed that initial values taken by dispersal traits have an influence on dispersal evolution, we can expect the evolution of dispersal in these snails will be different compared to the evolution of more generalist species of snails. This difference in dispersal capacity will undoubtedly have repercussions on species ability to evolve dispersal traits and adapt to global changes and associated extinction risks, and authors stress on the importance to consider the dispersal capacity of species when studying dispersal evolution (Dahirel et al. 2015). The capacity to perceive their environment and memorize it has also been demonstrated to have a significant impact on movement behaviours and subsequent evolution of dispersal traits (Zollner 2000, Olden et al. 2004, Pe'er and Kramer-Schadt 2008). For example, individuals may benefit from correctly identifying and memorizing the condition and locations of conspecifics or their density (Chaine and Clobert 2012), or the level of risk incurred in a given vegetation type (Biz et al. 2017). Thus, correctly accounting for dispersal capacity when modelling dispersal evolution in a given species is fundamental (Pe'er and Kramer-Schadt 2008). Finally, mating systems also have a strong effect on the evolution of dispersal, and need to be taken into account accurately when modelling dispersal evolution (Greenwood 1980, Duputié and Massol 2013).

❖ Alternative tactics

Moreover, individuals can display alternative dispersal tactics in the wild, as highlighted by this PhD thesis and several studies (Bonte et al. 2008a, Hogan and al. 2014), and these will definitely have an impact on the way selection acts on dispersal traits.

First, dispersal may imply different mediums, including terrestrial, aerial or marine pathways, for a single species (Fortuna et al. 2006, Bonte et al. 2008a). Depending on the selection pressures found in each ecosystem (see below), for example the destruction of dispersal pathways by urbanization or modified meteorological conditions, we should expect each tactic to be impacted at a different level. For example, I expect that an aerial dispersal tactic such as ballooning may not be impacted as much by human activities such as clear-cutting, which happens on the ground, however, this could impact more the tactic of rappelling in a species using these two tactics (Bell et al. 2005, Bonte et al. 2008a). Thus, the evolution of dispersal in a species presenting several alternative dispersal tactics should be a rather complex process, and should be modelled taking into account the different dispersal tactics an individual may display. Another example of alternative dispersal tactics may include passive versus active dispersal, in link with the medium used to disperse (Matthysen et al. 2012).

Second, if the dispersal process is heterogeneous within a population, individual traits should not be affected by selection equally, or at least not in the same time scale, as demonstrated by the results I presented in chapter IV. For example, a population where individuals have a strong tendency to disperse may be way more subjected to evolution compared to those which are low dispersers. Therefore, depending on the dispersal capacity of individuals, dispersal traits will evolve at varying rates and towards more or less high values, which may have effects on population dynamics (see below). For example, if tactics such as classic dispersal are highly represented in a population, whereby individuals usually move the longest distances and use a rather highly-correlated movement, we may expect the general tendency to have a highly-correlated movement to remain high for a longer period of time compared to a situation where initial tactics mainly comprise

individuals with low auto-correlation in movements such as the multi-range tactic. To better understand how these tactics may relate in terms of dispersal evolution, it would be very informative to be able to model the evolution of discrete dispersal tactics within a population. Lastly, tactics may vary spatially and temporally, which has mainly been demonstrated in plants (Buoro and Carlson 2014). Dispersal may occur at one or several stages in the life of an individual, and potentially simultaneously to other life history events. This has two implications for dispersing individuals. First, if dispersal occurs several times in the life of an individual, I expect the selection pressures may act more strongly on traits, because the factors exerting a selection pressure will act on trait selection several times in the life of the individual, as has also been suggested by Duputié and Massol (2013). These authors also explain that the timing of dispersal, i.e. the occurrence of dispersal at juvenile or adult stage, also has important repercussions on dispersal evolution. Thus, I expect that in cases where dispersal is more frequent in an individual's life, environmental pressures should lead to faster selection in that case. Second, I expect that if dispersal occurs concomitantly with potential reproductive events, and that, as a consequence, reproduction cannot occur, individuals will miss opportunities to transmit their genome. As a consequence, selection may not favour their traits compared to individuals for whom reproduction would not be impaired by dispersal, and so I conclude that species dynamics also have a strong impact on the way selection is applied, and the variation of dispersal costs associated to demographic traits should also have repercussions on dispersal evolution. For example, I showed that dispersers may perform less well in the context of climate change, notably incurring a reduction in their survival probability at the senescent stage, and thus, I expect their traits to be less selected for than their philopatric counterparts. In conclusion, I expect that if a given tactic leads to higher demographic costs, this tactic should be less selected for, because the associated traits at transfer phase will not be transmitted. Finally, invasive species are currently one of the main threats biodiversity is facing, and often disperse to expand their range. Several studies have already demonstrated that these species may display different movement tactics, for example between the core or range margins. Understanding which dispersal tactics these

species exhibit and examining their characteristics thus constitute a major challenge in order to better control their expansion (García-Berthou 2007, Václavík and Meentemeyer 2009, Harris et al. 2009).

b. Environmental characteristics

As I mentioned in the introduction, global change represents a large panel of threats to biodiversity. Fragmentation, pollution, predation or hunting, habitat destruction are all sorts of modifications of the environment which may impose different costs on dispersers (Bonte et al. 2012). Because these costs are varied, I expect dispersal to evolve differently with the type of environmental change that is occurring.

(i) Fragmentation

I showed in this PhD that dispersal movements should be more tortuous or short-distance when transience-associated mortality increased. However, other studies showed that in the case of habitat fragmentation, movement paths may become highly correlated and reduced dispersal propensity may evolve as a way to reduce the time spent in a risky habitat (Travis and Dytham 1999, Bonte et al. 2006, Schtickzelle et al. 2006, Cheptou et al. 2008, Ahlroth et al. 2010). This result may partly be explained by the percentage of suitable habitat that was modelled, as explained in the fourth chapter, but also because the selection pressure (fragmentation or increased mortality during transience) was different (although fragmentation should lead to an increase in mortality (Smith and Batzli 2006, Schtickzelle et al. 2006)). Fragmentation, or alternatively the level of landscape connectivity, may favour dispersal polymorphism, such as long and short-distance dispersal, and thus maintain the existence of alternative tactics to cope with environmental change (Bonte et al. 2010, Henriques-Silva et al. 2015). Moreover, the effects of global change should differ depending on which habitat environmental modifications are impacting. For example, deterioration of the natal habitat may lead to dispersal (Entling et al. 2011, Bestion et al. 2015, Van Hezewijk et al. 2018, Spaan et al.

2019) while alterations affecting transfer or settlement habitat may restrain dispersal (Schtickzelle et al. 2006, Awade and Metzger 2008, Bowler and Benton 2009). The outcome may also depend on the previous state of the habitat, for example, its previous degree of fragmentation (Cote et al. 2017).

(ii) Spatial and temporal heterogeneity in habitats

Second, habitat heterogeneity also influences the way selection acts on dispersal evolution (Fronhofer et al. 2014). In particular, spatial and temporal correlations may have contrasted effects. While increasing spatial correlation is expected to change the distribution of dispersal distances and lead to the selection of less dispersal events but of a higher dispersal distance, temporal autocorrelation selects for a reduced dispersal propensity (Travis 2001, Hanski et al. 2004, Bonte et al. 2010, Fronhofer et al. 2014, Burgess et al. 2015). Moreover, alternative strategies are more likely to exist when environmental conditions are variable, both at the spatial and temporal scales (Cote et al. 2017). This is consistent with the identification of alternative dispersal tactics in roe deer which appear to be driven by spatial environmental variability. For example, the propensity to adopt the classic dispersal tactic increased with habitat heterogeneity, human disturbance and high habitat quality, while the progressive dispersal tactic was rather exhibited in poor quality but less disturbed environments. Thus, I expect that the maintenance of diverse habitats in a landscape may benefit to the persistence of alternative dispersal strategies. However, if global change leads to a sort of homogenization of habitats, we may expect that some tactics may not be maintained.

(iii) Characteristics of environmental changes

The frequency, magnitude and predictability of environmental changes have also been demonstrated to impact dispersal evolution (Duputié and Massol 2013). Severe or unpredictable changes, including catastrophic events, should usually select for dispersal (Friedenberg 2003, Duputié and Massol 2013). Authors also demonstrated that the levels of predictability should influence dispersal propensity, with more individuals dispersing when environmental unpredictability is low (Hidalgo 2016). The type

of modification (direct mortality during transience, loss of suitable habitat, loss of sexual partners, poaching, etc.) may also have contrasted results: for example, habitat degradation may lead to an increase in dispersal propensity while habitat loss may lead to the opposite (North et al. 2011).

(iv) Mediums to disperse

Because dispersers may use different mediums to disperse (air, land, water), and because individuals may incur different costs in these environments (Burgess et al. 2015), I expect that selection pressures will act differently in these mediums. For example, fragmentation may lead to an increase in dispersal duration, and thus of energetic costs (Bonte et al. 2012, Benoît et al. 2019). This same environmental change (fragmentation) should however not have the same repercussions on species depending on the medium they use to disperse. For instance, swimming appears to be less costly compared with terrestrial displacements such as flying (Alexander et al. 1998), and thus, we may expect fragmentation to have more costs in terrestrial environments compared to marine ones. Moreover, each ecosystem also has its own characteristics which may lead to different dispersal barriers or costs, and thus, different repercussions on dispersal evolution. The medium used for dispersing thus has to be taken into account when studying the evolution of dispersal for a given species, and a new marine version of the software Rangeshifter should provide great avenues of research for studying the evolution of marine dispersal.

(v) Social factors

The effects of the environment on dispersal also comprise the effects of conspecifics. In particular, kin competition and inbreeding depression have been shown to elevate dispersal propensity, although dispersal costs may counteract their effect, or decrease immigration propensity (Cote and Clobert 2010, Hovestadt et al. 2012, Duputié and Massol 2013, Banks and Lindenmayer 2014, Hidalgo et al. 2016). These two factors may also lead to higher travelled distances during dispersal (Hovestadt et al. 2001, 2012, Burgess et al. 2015). In particular, inbreeding avoidance is at the origin of sex-

biased dispersal, if individuals of differing sex do not suffer the same costs (Duputié and Massol 2013). Moreover, low population sizes may also increase the propensity to disperse if they lead to an increase in extinction risk (Heino and Hanski 2001). Additionally, high density can be a strong driver of dispersal, for example to mitigate for competitive or agonistic interactions, but low density may also trigger dispersal if an Allee effect is present in the population, i.e. "a positive relationship between any component of individual fitness and either numbers or density of conspecific" (Stephens et al. 1999, Travis et al. 1999).

(vi) Combination of environmental changes

Lastly, evolution should also differ if populations incur a combination of environmental changes. Indeed, the few studies on the topic have suggested that the joint effects of two environmental changes may have significant impacts on dispersal (Cormont et al. 2011, Delattre et al. 2013). Thus, gathering information on how several environmental changes may impact dispersal costs should provide a clearer picture of how dispersal may evolve compared to actual knowledge based on the modelling of effects of only one source of environmental change.

Conclusion

As a conclusive point, dispersal is a highly heterogeneous process which could incur various costs depending on the actual tactic an individual is displaying. I identified six alternative tactics, but a whole range of other tactics may be expressed by dispersers depending on their life cycle or ecosystem type. This PhD thesis suggests that these tactics may imply varying costs, and that these costs vary with global change, leading to a decrease in individual fitness (see Fig. 13). For now, few studies have described the variations of dispersal costs with global changes, and thus, a large body of work remains to do to better comprehend how dispersal costs will continue to be affected in the future, and how they are going to impact population dynamics and persistence. Principle axes to

develop should include (1) describing with more detail the existence of dispersal costs at each of the dispersal phases, as most work on studying dispersal costs has been made on transience phase, (2) describing the variations of these costs with the main environmental change drivers (climate change and habitat degradation), to get more insight on the variety of responses dispersal costs may have with these changes, and (3) better characterising the impact of variations in dispersal costs with global changes on population dynamics and persistence, as for now, we have only little understanding of how populations will respond with variations in dispersal costs.

Increasing dispersal costs in the context of environmental changes are expected to have strong repercussions on population dynamics, and as such, they should be better addressed when studying dispersal evolution. Indeed, these costs will not only have effects on the short term but also at evolutionary timescales, and could lead to both a reduction in the success and geographical extent of dispersal. I emphasize that costs and their variations should be described as precisely as possible in future research as a way to predict more accurately how dispersal may evolve in a given environmental context. Finally, more work on the description of alternative dispersal tactics, in several model species, will also provide a better understanding of the entire range of variation in dispersal individuals could display in the face of global change, and the inclusion of these alternative tactics and costs into mechanistic modelling of dispersal will yield promising results to better understand and predict how species will cope with global change, and hence, protect them.

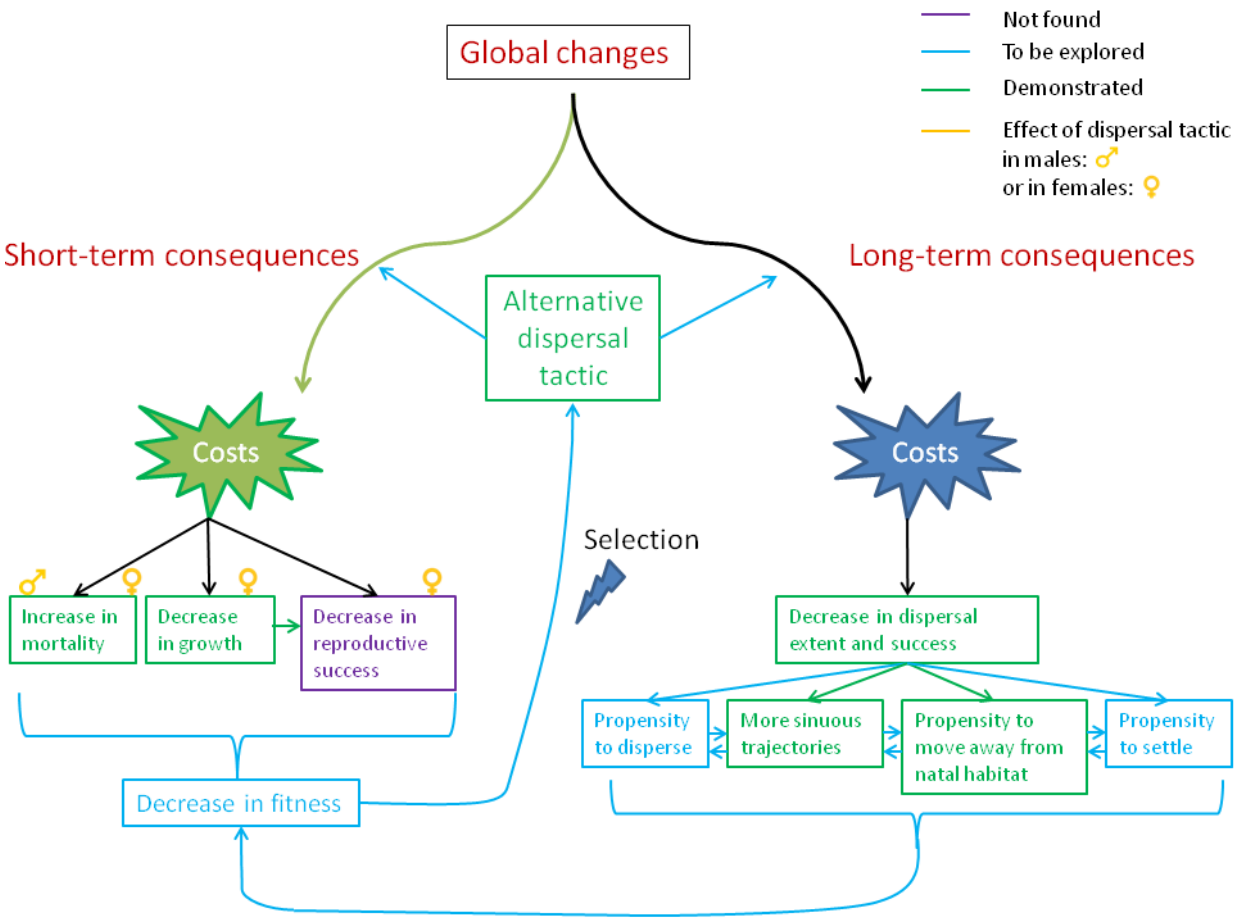


Fig. 13: Main conclusions from my PhD thesis. The impact of global changes on costs has both short and long-term consequences. Environmental changes lead to increased dispersal costs on the short term (here, in terms of survival, growth, and potentially reproduction as a cascading effect), which reduces individual fitness. Selection then operates to favour individuals with high fitness, which should reduce dispersal costs incurred because of global changes in the next generations. Addressing how a variety of environmental changes could impact dispersal costs is of high importance to determine how populations might persist in the future. On the long term, increasing dispersal costs due to global changes are expected to lead to the evolution of short-distance dispersal and to reduce dispersal success. Mechanistically, selection favours tortuous movements and individuals exhibiting a reduced bias to move away from their natal habitat during transfer phase. Determining the effects of dispersal costs on the joint evolution of dispersal traits constitutes a promising avenue of research. Arrows indicate the effect of one element on another. Colours inform if the relationships were demonstrated (green), not found (purple), or to be explored in further work (blue). Black arrows indicate non-studied interactions between two elements. Additionally, symbols (♂ and ♀) mention if, for a given sex, an effect of dispersal status influenced the relationship between a cost and a demographic parameter.

References

Laura Benoït

Aars, J., & Ims, R. A. (1999). The effect of habitat corridors on rates of transfer and interbreeding between vole demes. *Ecology*, *80*(5), 1648-1655.

Aars, J., Johannesen, E., & Ims, R. A. (1999). Demographic consequences of movements in subdivided root vole populations. *Oikos*, 204-216.

Adamo, S. A., Roberts, J. L., Easy, R. H., & Ross, N. W. (2008). Competition between immune function and lipid transport for the protein apolipophorin III leads to stress-induced immunosuppression in crickets. *Journal of Experimental Biology*, 211(4), 531-538.

Addis, B. R., Tobalske, B. W., Davenport, J. M., & Lowe, W. H. (2019). A distance–performance trade-off in the phenotypic basis of dispersal. *Ecology and Evolution*, 9(18), 10644-10653.

Aguillon, S. M., & Duckworth, R. A. (2015). Kin aggression and resource availability influence phenotype-dependent dispersal in a passerine bird. *Behavioral ecology and sociobiology*, *69*(4), 625-633.

Ahlroth, P., Alatalo, R. V., & Suhonen, J. (2010). Reduced dispersal propensity in the wingless waterstrider Aquarius najas in a highly fragmented landscape. *Oecologia*, *162*(2), 323-330.

Alberti, M., Correa, C., Marzluff, J. M., Hendry, A. P., Palkovacs, E. P., Gotanda, K. M., ... & Zhou, Y. (2017). Global urban signatures of phenotypic change in animal and plant populations. *Proceedings of the National Academy of Sciences*, *114*(34), 8951-8956.

Alberts, S. C., & Altmann, J. (1995). Balancing costs and opportunities: dispersal in male baboons. *The American Naturalist*, *145*(2), 279-306.

Alexander, R. M., (1998). When is migration worthwhile for animals that walk, swim or fly?. *Journal of Avian Biology*, 387-394.

Allen, C. D., Macalady, A. K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., ... & Gonzalez, P. (2010). A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest ecology and management*, *259*(4), 660-684.

Altwegg, R., Ringsby, T. H., & SÆther, B. E. (2000). Phenotypic correlates and consequences of dispersal in a metapopulation of house sparrows Passer domesticus. *Journal of Animal Ecology*, 69(5), 762-770.

Alves, J. A., Sutherland, W. J., & Gill, J. A. (2011). Will improving wastewater treatment impact shorebirds? Effects of sewage discharges on estuarine invertebrates and birds. Animal Conservation, 15(1), 44-52.

Amarasekare, P. (2004). The role of density-dependent dispersal in source–sink dynamics. *Journal of theoretical biology*, *226*(2), 159-168.

Andersen, R., Duncan, P., & Linnell, J. D. (Eds.). (1998). The European roe deer: the biology of success.

Anderson, B. J., Akçakaya, H. R., Araújo, M. B., Fordham, D. A., Martinez-Meyer, E., Thuiller, W., & Brook, B. W. (2009). Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1661), 1415-1420.

Angelier, F., & Wingfield, J. C. (2013). Importance of the glucocorticoid stress response in a changing world: theory, hypotheses and perspectives. *General and comparative endocrinology*, *190*, 118-128.

Arendt, J. D. (2015). Effects of dispersal plasticity on population divergence and speciation. *Heredity*, *115*(4), 306.

Arnold. W. (1990). The evolution of marmot sociality: I. Why disperse late?. *Behavioral Ecology and Sociobiology*, *27*(4), 229-237.

Atkins, J. L., Perry, G. L., & Dennis, T. E. (2019). Effects of mis-alignment between dispersal traits and landscape structure on dispersal success in fragmented landscapes. *Royal Society open science*, *6*(1), 181702.

Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Campbell-Nelson, S., Robertson, K. W., & Ketterson, E. D. (2012). Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behavioral Ecology*, *23*(5), 960-969.

Awade, M., & Metzger, J. P. (2008). Using gap-crossing capacity to evaluate functional connectivity of two Atlantic rainforest birds and their response to fragmentation. *Austral Ecology*, *33*(7), 863-871.

Awade, M., Candia-Gallardo, C., Cornelius, C., & Metzger, J. P. (2017). High emigration propensity and low mortality on transfer drives female-biased dispersal of Pyriglena leucoptera in fragmented landscapes. *PloS one*, *12*(1), e0170493.

[AWCRT] Alberta Woodland Caribou Recovery Team. 2005. Alberta Woodland Caribou Recovery Plan, 2004/05–2013/14. Alberta Sustainable Resource Development, Fish and Wildlife Division.

Backlund, P., Janetos, A., & Schimel, D. (2008). The effects of climate change on agriculture, land resources, water resources, and biodiversity in the United States. Synthesis and Assessment Product 4.3. *Washington, DC: US Environmental Protection Agency, Climate Change Science Program*. 240 p.

Bacles, C. F., Lowe, A. J., & Ennos, R. A. (2006). Effective seed dispersal across a fragmented landscape. *Science*, 311(5761), 628-628.

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, *88*(2), 310-326.

Baines, C. B., & McCauley, S. J. (2018). Natal habitat conditions have carryover effects on dispersal capacity and behavior. *Ecosphere*, *9*(10), e02465.

Balmford, A., Beresford, J., Green, J., Naidoo, R., Walpole, M., & Manica, A. (2009). A global perspective on trends in nature-based tourism. *PLoS biology*, *7*(6), e1000144.

Banks, S. C., & Lindenmayer, D. B. (2014). Inbreeding avoidance, patch isolation and matrix permeability influence dispersal and settlement choices by male agile antechinus in a fragmented landscape. *Journal of Animal Ecology*, *83*(2), 515-524.

Barbraud, C., Johnson, A. R., & Bertault, G. (2003). Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. *Journal of Animal Ecology*, *72*(2), 246-257.

Bartomeus, I., Ascher, J. S., Wagner, D., Danforth, B. N., Colla, S., Kornbluth, S., & Winfree, R. (2011). Climate-associated phenological advances in bee pollinators and bee-pollinated plants. *Proceedings of the National Academy of Sciences*, *108*(51), 20645-20649.

Barton, K. A., Phillips, B. L., Morales, J. M., & Travis, J. M. (2009). The evolution of an 'intelligent'dispersal strategy: biased, correlated random walks in patchy landscapes. *Oikos*, *118*(2), 309-319.

Bartoń, K. A., Hovestadt, T., Phillips, B. L., & Travis, J. M. J. (2012). Risky movement increases the rate of range expansion. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1731), 1194-1202.

Bates, A. J., Sadler, J. P., & Fowles, A. P. (2006). Condition-dependent dispersal of a patchily distributed riparian ground beetle in response to disturbance. *Oecologia*, *150*(1), 50-60.

Becker, M., McRobb, R., Watson, F., Droge, E., Kanyembo, B., Murdoch, J., & Kakumbi, C. (2013). Evaluating wire-snare poaching trends and the impacts of by-catch on elephants and large carnivores. *Biological Conservation*, *158*, 26-36.

Bell, J. R., Bohan, D. A., Shaw, E. M., & Weyman, G. S. (2005). Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bulletin of entomological research*, *95*(2), 69-114.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology letters*, *15*(4), 365-377.

Bellard, C., Cassey, P., & Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology letters*, *12*(2), 20150623.

Benard, M. F., & McCauley, S. J. (2008). Integrating across life-history stages: consequences of natal habitat effects on dispersal. *The American Naturalist*, 171(5), 553-567.

Benoit, L., Hewison, A. M., Coulon, A., Debeffe, L., Grémillet, D., Ducros, D., ... & Morellet, N. (2019). Accelerating across the landscape: the energetic costs of natal dispersal in a large herbivore. *Journal of Animal Ecology*.

Benton, T. G., & Bowler, D. E. (2012). Linking dispersal to spatial dynamics. *Dispersal ecology and evolution*, *251*, 265.

Berg, M. P., Kiers, E. T., Driessen, G., Van Der HEIJDEN, M. A. R. C. E. L., Kooi, B. W., Kuenen, F., ... & Ellers, J. (2010). Adapt or disperse: understanding species persistence in a changing world. *Global Change Biology*, *16*(2), 587-598.

Berger, V., Lemaître, J. F., Dupont, P., Allainé, D., Gaillard, J. M., & Cohas, A. (2016). Age-specific survival in the socially monogamous alpine marmot (*Marmota marmota*): evidence of senescence. *Journal of Mammalogy*, *97*(3), 992-1000.

Bertolino, S., & Genovesi, P. (2003). Spread and attempted eradication of the grey squirrel (Sciurus carolinensis) in Italy, and consequences for the red squirrel *(Sciurus vulgaris*) in Eurasia. *Biological Conservation*, *109*(3), 351-358.

Bestion, E., Clobert, J., & Cote, J. (2015). Dispersal response to climate change: scaling down to intraspecific variation. *Ecology Letters*, *18*(11), 1226-1233.

Bieber, C., & Ruf, T. (2005). Population dynamics in wild boar *Sus scrofa*: ecology, elasticity of growth rate and implications for the management of pulsed resource consumers. *Journal of Applied Ecology*, *42*(6), 1203-1213.

Biggs, D., Courchamp, F., Martin, R., & Possingham, H. P. (2013). Legal trade of Africa's rhino horns. *Science*, *339*(6123), 1038-1039.

Biz, M., Cornelius, C., & Metzger, J. P. W. (2017). Matrix type affects movement behavior of a Neotropical understory forest bird. *Perspectives in Ecology and Conservation*, *15*(1), 10-17.

Bocedi, G., Heinonen, J., & Travis, J. M. (2012). Uncertainty and the role of information acquisition in the evolution of context-dependent emigration. *The American Naturalist*, *179*(5), 606-620.

Bohonak, A. J. (1999). Dispersal, gene flow, and population structure. *The Quarterly Review of Biology*, *74*(1), 21-45.

Bolger, D. T., Patten, M. A., & Bostock, D. C. (2005). Avian reproductive failure in response to an extreme climatic event. *Oecologia*, *142*(3), 398-406.

Bonnet, T., Morrissey, M. B., Morris, A., Morris, S., Clutton-Brock, T. H., Pemberton, J. M., & Kruuk, L. E. (2019). The role of selection and evolution in changing parturition date in a red deer population. *PLoS biology*, 17(11).

Bonte, D., Vandenbroecke, N., Lens, L., & Maelfait, J. P. (2003). Low propensity for aerial dispersal in specialist spiders from fragmented landscapes. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1524), 1601-1607.

Bonte, D., Bossuyt, B., & Lens, L. (2007). Aerial dispersal plasticity under different wind velocities in a salt marsh wolf spider. *Behavioral Ecology*, *18*(2), 438-443.

Bonte, D., Travis, J. M., De Clercq, N., Zwertvaegher, I., & Lens, L. (2008a). Thermal conditions during juvenile development affect adult dispersal in a spider. *Proceedings of the National Academy of Sciences*, *105*(44), 17000-17005.

Bonte, D., Lukáč, M., & Lens, L. (2008b). Starvation affects pre-dispersal behaviour of Erigone spiders. *Basic and Applied Ecology*, *9*(3), 308-315.

Bonte, D. (2009). Inbreeding depresses short and long distance dispersal in three congeneric spiders. *Journal of Evolutionary Biology*, *22*(7), 1429-1434.

Bonte, D., Hovestadt, T., & Poethke, H. J. (2010). Evolution of dispersal polymorphism and local adaptation of dispersal distance in spatially structured landscapes. *Oikos*, *119*(3), 560-566.

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., ... & Schtickzelle, N. (2012). Costs of dispersal. *Biological Reviews*, *87*(2), 290-312.

Bonte, D., De Roissart, A., Wybouw, N., & Van Leeuwen, T. (2014). Fitness maximization by dispersal: evidence from an invasion experiment. *Ecology*, *95*(11), 3104-3111.

Both, C., Artemyev, A. V., Blaauw, B., Cowie, R. J., Dekhuijzen, A. J., Eeva, T., ... & Metcalfe, N. B. (2004). Large–scale geographical variation confirms that climate change causes birds to lay earlier. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1549), 1657-1662.

Bötsch, Y., Tablado, Z., & Jenni, L. (2017). Experimental evidence of human recreational disturbance effects on bird-territory establishment. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1858), 20170846.

Boulinier, T., McCoy, K. D., Yoccoz, N. G., Gasparini, J., & Tveraa, T. (2008). Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. *Biology Letters*, *4*(5), 538-540.

Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews*, *80*(2), 205-225.

Bowler, D. E., & Benton, T. G. (2009). Variation in dispersal mortality and dispersal propensity among individuals: the effects of age, sex and resource availability. *Journal of Animal Ecology*, *78*(6), 1234-1241.

Bradshaw, W. E., & Holzapfel, C. M. (2006). Evolutionary response to rapid climate change. *Science*, *312*(5779), 1477-1478.

Braendle, C., Davis, G. K., Brisson, J. A., & Stern, D. L. (2006). Wing dimorphism in aphids. *Heredity*, *97*(3), 192-199.

Brashares, J. S., Arcese, P., Sam, M. K., Coppolillo, P. B., Sinclair, A. R., & Balmford, A. (2004). Bushmeat hunting, wildlife declines, and fish supply in West Africa. *Science*, *306*(5699), 1180-1183.

Brodie, J. F., Helmy, O. E., Brockelman, W. Y., & Maron, J. L. (2009). Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecological Applications*, *19*(4), 854-863.

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. (2008). Synergies among extinction drivers under global change. *Trends in ecology & evolution*, *23*(8), 453-460.

Brown et al. 1992: Brown, G. E., Brown, J. A., & Srivastava, R. K. (1992). The effect of stocking density on the behaviour of Arctic charr (*Salvelinus alpinus* L.). *Journal of Fish Biology*, *41*(6), 955-963.

Brown, L. R., Gray, R. H., Hughes, R. M., & Meador, M. R. (2005). Introduction to effects of urbanization on stream ecosystems. In *American Fisheries Society Symposium* (Vol. 47, No. 1-8).

Brown, M. J., & Paxton, R. J. (2009). The conservation of bees: a global perspective. *Apidologie*, *40*(3), 410-416.

Brown, L. M., & Crone, E. E. (2016). Individual variation changes dispersal distance and area requirements of a checkerspot butterfly. *Ecology*, *97*(1), 106-115.

Bruinderink, G. G., & Hazebroek, E. (1996). Ungulate traffic collisions in Europe. *Conservation biology*, 10(4), 1059-1067.

Buckley, L. B., Ehrenberger, J. C., & Angilletta Jr, M. J. (2015). Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change. *Functional Ecology*, *29*(8), 1038-1047.

Buoro, M., & Carlson, S. M. (2014). Life-history syndromes: Integrating dispersal through space and time. *Ecology Letters*, *17*(6), 756-767.

Burbaiteė, L., & Csányi, S. (2009). Roe deer population and harvest changes in Europe. *Estonian Journal of Ecology*, 58(3).

Burgess, S. C., Treml, E. A., & Marshall, D. J. (2012). How do dispersal costs and habitat selection influence realized population connectivity?. *Ecology*, 93(6), 1378-1387.

Burgess, S. C., Baskett, M. L., Grosberg, R. K., Morgan, S. G., & Strathmann, R. R. (2015). When is dispersal for dispersal? Unifying marine and terrestrial perspectives. *Biological Reviews*, *91*(3), 867-882.

Buskey, E. J., White, H. K., & Esbaugh, A. J. (2016). Impact of oil spills on marine life in the Gulf of Mexico: effects on plankton, nekton, and deep-sea benthos. *Oceanography*, *29*(3), 174-181.

Cadenasso, M. L., Pickett, S. T. A., Groffman, P. M., Band, L. E., Brush, G. S., Galvin, M. F., ... & O'Neil-Dunne, J. P. M. (2008). Exchanges across Land-Water-Scape Boundaries in Urban Systems: Strategies for Reducing Nitrate Pollution. *Annals of the New York Academy of Sciences*, *1134*(1), 213-232.

Cañete, J. I., Gallardo, C. S., Romero, M., & Ambler, R. (2007). Planktonic drifting dispersal of early juvenile Trochita calyptraeaformis Born 1778 [Gastropoda: Calyptraeidae]. *Journal of Experimental Marine Biology and Ecology*, *346*(1-2), 1-7.

Cant, M. A., Otali, E., & Mwanguhya, F. (2001). Eviction and dispersal in co-operatively breeding banded mongooses (*Mungos mungo*). *Journal of Zoology*, *254*(2), 155-162.

Castellón, T. D., & Sieving, K. E. (2006). An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conservation biology*, *20*(1), 135-145.

Caswell, H. (1978). A general formula for the sensitivity of population growth rate to changes in life history parameters. *Theoretical population biology*, *14*(2), 215-230.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science advances*, *1*(5), e1400253.

Chaine, A. S., & Clobert, J. (2012). Dispersal. *Behavioural responses to a changing world: Mechanisms and consequences*, 63e79.

Challender, D. W. (2011). Asian pangolins: increasing affluence driving hunting pressure. *Traffic Bulletin*, *23*(3), 92-93.

Chaput-Bardy, A., Grégoire, A., Baguette, M., Pagano, A., & Secondi, J. (2010). Condition and phenotype-dependent dispersal in a damselfly, Calopteryx splendens. *PloS one*, *5*(5), e10694.

Charmantier, A., & Gienapp, P. (2014). Climate change and timing of avian breeding and migration: evolutionary versus plastic changes. *Evolutionary Applications*, 7(1), 15-28.

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*(6045), 1024-1026.

Cheptou, P. O., Carrue, O., Rouifed, S., & Cantarel, A. (2008). Rapid evolution of seed dispersal in an urban environment in the weed *Crepis sancta*. *Proceedings of the National Academy of Sciences*, *105*(10), 3796-3799.

Cheptou, P. O., & Massol, F. (2009). Pollination fluctuations drive evolutionary syndromes linking dispersal and mating system. *The American Naturalist*, *174*(1), 46-55.

Cheptou, P. O., Hargreaves, A. L., Bonte, D., & Jacquemyn, H. (2017). Adaptation to fragmentation: evolutionary dynamics driven by human influences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1712), 20160037.

Cheung, W. W., Lam, V. W., Sarmiento, J. L., Kearney, K., Watson, R., & Pauly, D. (2009). Projecting global marine biodiversity impacts under climate change scenarios. *Fish and fisheries*, *10*(3), 235-251.

Chevin, L. M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLoS biology*, *8*(4), e1000357.

Cho, M., Neubauer, P., Fahrenson, C., & Rechenberg, I. (2018). An observational study of ballooning in large spiders: Nanoscale multifibers enable large spiders' soaring flight. *PLoS biology*, 16(6), e2004405.

Church, J. A., Clark, P. U., Cazenave, A., Gregory, J. M., Jevrejeva, S., Levermann, A., ... & Payne, A. J. (2013). *Sea level change*. PM Cambridge University Press.

Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J.D. (2001) Dispersal. Oxford University Press, Oxford.

Clobert, J., Ims, R. A., & Rousset, F. (2004). Causes, mechanisms and consequences of dispersal. In *Ecology, genetics and evolution of metapopulations* (pp. 307-335). Academic Press.

Clobert, J., Le Galliard, J. F., Cote, J., Meylan, S., & Massot, M. (2009). Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology letters*, *12*(3), 197-209.

Clobert, J., Baguette, M., Benton, T. G., & Bullock, J. M. (Eds.). (2012). *Dispersal ecology and evolution*. Oxford University Press.

Clutton-Brock, T. (2007). Sexual selection in males and females. *Science*, *318*(5858), 1882-1885.

Coates, W. D., Hale, R., & Morrongiello, J. R. (2019). Dispersal decisions and personality in a freshwater fish. *Animal Behaviour*, *157*, 209-218.

Cooper, E. B., Taylor, R. W., Kelley, A. D., Martinig, A. R., Boutin, S., Humphries, M. M., ... & McAdam, A. G. (2017). Personality is correlated with natal dispersal in North American red squirrels (*Tamiasciurus hudsonicus*). *Behaviour*, *154*(9-10), 939-961.

Coppack, T., & Pulido, F. (2004). Photoperiodic response and the adaptability of avian life cycles to environmental change. *Advances in Ecological Research*, *35*, 131-150.

Cormont, A., Malinowska, A. H., Kostenko, O., Radchuk, V., Hemerik, L., WallisDeVries, M. F., & Verboom, J. (2011). Effect of local weather on butterfly flight behaviour, movement, and colonization: significance for dispersal under climate change. *Biodiversity and Conservation*, *20*(3), 483-503.

Cosentino, B. J., Schooley, R. L., & Phillips, C. A. (2011). Connectivity of agroecosystems: dispersal costs can vary among crops. *Landscape ecology*, *26*(3), 371-379.

Cote, J., & Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 383-390.

Cote, J., & Clobert, J. (2010). Risky dispersal: avoiding kin competition despite uncertainty. *Ecology*, *91*(5), 1485-1493.

Cote, J., Clobert, J., Brodin, T., Fogarty, S., & Sih, A. (2010). Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4065-4076.

Cote, J., Fogarty, S., Brodin, T., Weinersmith, K., & Sih, A. (2011). Personality-dependent dispersal in the invasive mosquitofish: group composition matters. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1712), 1670-1678.

Cote, J., Bestion, E., Jacob, S., Travis, J., Legrand, D., & Baguette, M. (2017). Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. *Ecography*, *40*(1), 56-73.

Coulon, A., Cosson, J. F., Angibault, J. M., Cargnelutti, B., Galan, M., Morellet, N., ... & Hewison, A. J. M. (2004). Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: an individual–based approach. *Molecular ecology*, *13*(9), 2841-2850.

Coulon, A., Cosson, J. F., Morellet, N., Angibault, J. M., Cargnelutti, B., Galan, M., ... & Hewison, A. J. M. (2006). Dispersal is not female biased in a resource-defence mating ungulate, the European roe deer. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1584), 341-348.

Coulon, A., Fitzpatrick, J. W., Bowman, R., & Lovette, I. J. (2010). Effects of habitat fragmentation on effective dispersal of Florida Scrub-Jays. *Conservation Biology*, *24*(4), 1080-1088.

Couriot, O., Hewison, A. M., Saïd, S., Cagnacci, F., Chamaillé-Jammes, S., Linnell, J. D., ... & Kjellander, P. (2018). Truly sedentary? The multi-range tactic as a response to resource heterogeneity and unpredictability in a large herbivore. *Oecologia*, *187*(1), 47-60.

Cox, A. S., & Kesler, D. C. (2012). Prospecting behavior and the influenceof forest cover on natal dispersal in aresident bird. *Behavioral Ecology*, *23*(5), 1068-1077.

Crooks, K. R., Burdett, C. L., Theobald, D. M., Rondinini, C., & Boitani, L. (2011). Global patterns of fragmentation and connectivity of mammalian carnivore habitat. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366(1578), 2642-2651.

Dahirel, M., Olivier, E., Guiller, A., Martin, M. C., Madec, L., & Ansart, A. (2015). Movement propensity and ability correlate with ecological specialization in European land snails: comparative analysis of a dispersal syndrome. *Journal of Animal Ecology*, *84*(1), 228-238.

Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature climate change*, *3*(1), 52.

Danchin, E., & Cam, E. (2002). Can non-breeding be a cost of breeding dispersal?. *Behavioral Ecology and Sociobiology*, *51*(2), 153-163.

David, G., Giffard, B., Piou, D., & Jactel, H. (2013). Dispersal capacity of Monochamus galloprovincialis, the European vector of the pine wood nematode, on flight mills. *Journal of Applied Entomology*, *138*(8), 566-576.

Davis, J. M., & Stamps, J. A. (2004). The effect of natal experience on habitat preferences. *Trends in ecology & evolution*, 19(8), 411-416.

Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C., & Mace, G. M. (2011). Beyond predictions: biodiversity conservation in a changing climate. *science*, *332*(6025), 53-58.

Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Bon, R., Gaillard, J. M., & Mark Hewison, A. J. (2012). Condition-dependent natal dispersal in a large herbivore: heavier animals show a greater propensity to disperse and travel further. *Journal of Animal Ecology*, *81*(6), 1327-1327.

Debeffe, L., Morellet, N., Cargnelutti, B., Lourtet, B., Coulon, A., Gaillard, J. M., ... & Hewison, A. J. M. (2013). Exploration as a key component of natal dispersal: dispersers explore more than philopatric individuals in roe deer. *Animal Behaviour*, 86(1), 143-151.

Debeffe, L., Morellet, N., Bonnot, N., Gaillard, J. M., Cargnelutti, B., Verheyden-Tixier, H., ... & Hewison, A. J. M. (2014). The link between behavioural type and natal dispersal propensity reveals a dispersal syndrome in a large herbivore. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1790), 20140873.

Debeffe, L., Richard, E., Medill, S. A., Weisgerber, J. N., & McLoughlin, P. D. (2015). Costs of social dispersal in a polygynous mammal. *Behavioral Ecology*, *26*(6), 1476-1485.

Delattre, T., Baguette, M., Burel, F., Stevens, V. M., Quénol, H., & Vernon, P. (2013). Interactive effects of landscape and weather on dispersal. *Oikos*, *122*(11), 1576-1585.

Delgado, M. D. M., Penteriani, V., Revilla, E., & Nams, V. O. (2010). The effect of phenotypic traits and external cues on natal dispersal movements. *Journal of Animal Ecology*, 79(3), 620-632.

Delgado, M. D. M., Bartoń, K. A., Bonte, D., & Travis, J. M. J. (2014). Prospecting and dispersal: their eco-evolutionary dynamics and implications for population patterns. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1778), 20132851.

Den Boer, P. (1968). Spreading of risk and stabilization of animal numbers. *Acta biotheoretica*, *18*(1), 165-194.

Denoël, M., Dalleur, S., Langrand, E., Besnard, A., & Cayuela, H. (2018). Dispersal and alternative breeding site fidelity strategies in an amphibian. *Ecography*, *41*(9), 1543-1555.

Descamps, S., Aars, J., Fuglei, E., Kovacs, K. M., Lydersen, C., Pavlova, O., ... & Strøm, H. (2017). Climate change impacts on wildlife in a High Arctic archipelago–Svalbard, Norway. *Global Change Biology*, *23*(2), 490-502.

Devictor, V., Julliard, R., Couvet, D., & Jiguet, F. (2008). Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society B: Biological Sciences*, 275(1652), 2743-2748.

DeWitt, T. J., Sih, A., & Wilson, D. S. (1998). Costs and limits of phenotypic plasticity. *Trends in ecology & evolution*, 13(2), 77-81.

Dickie, M., Serrouya, R., McNay, R. S., & Boutin, S. (2017). Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology*, *54*(1), 253-263.

Dingemanse, N. J., Both, C., Van Noordwijk, A. J., Rutten, A. L., & Drent, P. J. (2003). Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1516), 741-747.

Dingemanse, N. J., Moiron, M., Araya-Ajoy, Y. G., Mouchet, A., & Abbey-Lee, R. N. (2019). Individual variation in age-dependent reproduction: fast explorers live fast but senesce young?. *Journal of Animal Ecology*.

Dittmann, T., Zinsmeister, D., & Becker, P. H. (2005). Dispersal decisions: common terns, *Sterna hirundo*, choose between colonies during prospecting. *Animal behaviour*, *70*(1), 13-20.

Dixon, J. D., Oli, M. K., Wooten, M. C., Eason, T. H., McCown, J. W., & Paetkau, D. (2006). Effectiveness of a regional corridor in connecting two Florida black bear populations. *Conservation biology*, 20(1), 155-162.

Doligez, B., Gustafsson, L., & Pärt, T. (2009). 'Heritability'of dispersal propensity in a patchy population. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1668), 2829-2836.

Doney, S. C., Ruckelshaus, M., Duffy, J. E., Barry, J. P., Chan, F., English, C. A., ... & Polovina, J. (2012). *Climate change impacts on marine ecosystems*.

Droghini, A., & Boutin, S. (2017). Snow conditions influence grey wolf (*Canis lupus*) travel paths: the effect of human-created linear features. *Canadian Journal of Zoology*, *96*(1), 39-47.

Duckworth, R. A., & Badyaev, A. V. (2007). Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences*, *104*(38), 15017-15022.

Duputié, A., & Massol, F. (2013). An empiricist's guide to theoretical predictions on the evolution of dispersal. *Interface focus*, *3*(6), 20130028.

Duriez, O., Sæther, S. A., Ens, B. J., Choquet, R., Pradel, R., Lambeck, R. H., & Klaassen, M. (2009). Estimating survival and movements using both live and dead recoveries: a case study of oystercatchers confronted with habitat change. *Journal of Applied Ecology*, *46*(1), 144-153.

Dytham, C. (2009). Evolved dispersal strategies at range margins. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1661), 1407-1413.

Edelsparre, A. H., Shahid, A., & Fitzpatrick, M. J. (2018). Habitat connectivity is determined by the scale of habitat loss and dispersal strategy. *Ecology and evolution*, *8*(11), 5508-5514.

Edwards, M., & Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, *430*(7002), 881.

Ekernas, L. S., & Cords, M. (2007). Social and environmental factors influencing natal dispersal in blue monkeys, *Cercopithecus mitis stuhlmanni*. *Animal Behaviour*, *73*(6), 1009-1020.

Eikenaar, C., Richardson, D. S., Brouwer, L., & Komdeur, J. (2007). Parent presence, delayed dispersal, and territory acquisition in the Seychelles warbler. *Behavioral Ecology*, *18*(5), 874-879.

Eizaguirre, C., & Baltazar-Soares, M. (2014). Evolutionary conservation—evaluating the adaptive potential of species. *Evolutionary Applications*, *7*(9), 963-967.

Entling, M. H., Stämpfli, K., & Ovaskainen, O. (2011). Increased propensity for aerial dispersal in disturbed habitats due to intraspecific variation and species turnover. *Oikos*, *120*(7), 1099-1109.

Fattorini, S. (2011). Insect extinction by urbanization: a long term study in Rome. *Biological Conservation*, *144*(1), 370-375.

Feely, R. A., Doney, S. C., & Cooley, S. R. (2009). Ocean acidification: Present conditions and future changes in a high-CO_2 world. *Oceanography*, *22*(4), 36-47.

Ferreras, P., Aldama, J. J., Beltrán, J. F., & Delibes, M. (1992). Rates and causes of mortality in a fragmented population of Iberian lynx *Felis pardina* Temminck, 1824. *Biological conservation*, *61*(3), 197-202.

Ferriere, R., Belthoff, J. R., Olivieri, I., & Krackow, S. (2000). Evolving dispersal: where to go next?. *Trends in Ecology & Evolution*, *15*(1), 5-7.

Figuerola, J. (2007). Climate and dispersal: black-winged stilts disperse further in dry springs. *PLoS One*, *2*(6), e539.

Fitzherbert, E. B., Struebig, M. J., Morel, A., Danielsen, F., Brühl, C. A., Donald, P. F., & Phalan, B. (2008). How will oil palm expansion affect biodiversity?. *Trends in ecology & evolution*, *23*(10), 538-545.

Firebaugh, A., & Haynes, K. J. (2016). Experimental tests of light-pollution impacts on nocturnal insect courtship and dispersal. *Oecologia*, *182*(4), 1203-1211.

Flaherty, M., & Lawton, C. (2019). The regional demise of a non-native invasive species: the decline of grey squirrels in Ireland. *Biological Invasions*, *21*(7), 2401-2416.

Fleming, I. A., & Johansen, P. H. (1984). Density and agonistic behaviour in young-of-the-year largemouth bass (*Micropterus salmoides*). *Canadian journal of zoology*, *62*(8), 1454-1455.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., ... & Helkowski, J. H. (2005). Global consequences of land use. *science*, *309*(5734), 570-574.

Fontúrbel, F. E., Candia, A. B., Malebrán, J., Salazar, D. A., González-Browne, C., & Medel, R. (2015). Meta-analysis of anthropogenic habitat disturbance effects on animal-mediated seed dispersal. *Global Change Biology*, 21(11), 3951-3960.

Forbes, S. H., & Boyd, D. K. (1997). Genetic Structure and Migration in Native and Reintroduced Rocky Mountain Wolf Populations: Estructura Genética y Migración de Poblaciones Nativas y Reintroducidas del Lobo de las Montañas Rocallosas. *Conservation Biology*, *11*(5), 1226-1234.

Fortuna, M. A., Gómez-Rodríguez, C., & Bascompte, J. (2006). Spatial network structure and amphibian persistence in stochastic environments. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1592), 1429-1434.

Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N., & Skalski, G. T. (2001). Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *The American Naturalist*, *158*(2), 124-135.

Friedenberg, N. A. (2003). Experimental evolution of dispersal in spatiotemporally variable microcosms. *Ecology Letters*, *6*(10), 953-959.

Fronhofer, E. A., Stelz, J. M., Lutz, E., Poethke, H. J., & Bonte, D. (2014). Spatially correlated extinctions select for less emigration but larger dispersal distances in the spider mite *Tetranychus urticae*. *Evolution*, *68*(6), 1838-1844.

Fronhofer, E. A., Legrand, D., Altermatt, F., Ansart, A., Blanchet, S., Bonte, D., ... & Di Gesu, L. (2018). Bottom-up and top-down control of dispersal across major organismal groups. *Nature ecology & evolution*, *2*(12), 1859.

Gaillard, J. M., Sempéré, A. J., Boutin, J. M., Laere, G. V., & Boisaubert, B. (1992). Effects of age and body weight on the proportion of females breeding in a population of roe deer (*Capreolus capreolus*). *Canadian Journal of Zoology*, *70*(8), 1541-1545.

Gaillard, J. M., & Yoccoz, N. G. (2003). Temporal variation in survival of mammals: a case of environmental canalization?. *Ecology*, *84*(12), 3294-3306.

Gaillard, J. M., Festa-Bianchet, M., Yoccoz, N. G., Loison, A., & Toigo, C. (2000). Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of ecology and Systematics*, *31*(1), 367-393.

Gaillard, J. M., Hewison, A. J. M., Kjellander, P., Pettorelli, N., Bonenfant, C., Van Moorter, B., ... & Angibault, J. M. (2008). Population density and sex do not influence fine-scale natal dispersal in roe deer. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1646), 2025-2030.

Gaillard, J. M., Mark Hewison, A. J., Klein, F., Plard, F., Douhard, M., Davison, R., & Bonenfant, C. (2013). How does climate change influence demographic processes of widespread species? Lessons from the comparative analysis of contrasted populations of roe deer. *Ecology letters*, *16*, 48-57.

Gamble, L. R., McGarigal, K., & Compton, B. W. (2007). Fidelity and dispersal in the pond-breeding amphibian, Ambystoma opacum: implications for spatio-temporal population dynamics and conservation. *Biological Conservation*, *139*(3-4), 247-257.

Garant, D., Kruuk, L. E., Wilkin, T. A., McCleery, R. H., & Sheldon, B. C. (2005). Evolution driven by differential dispersal within a wild bird population. *Nature*, 433(7021), 60.

Garant, D. A. N. Y., Forde, S. E., & Hendry, A. P. (2007). The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology*, *21*(3), 434-443.

García-Berthou, E. (2007). The characteristics of invasive fishes: what has been learned so far?. *Journal of Fish Biology*, *71*, 33-55.

Gardner, R. H., & Gustafson, E. J. (2004). Simulating dispersal of reintroduced species within heterogeneous landscapes. *Ecological Modelling*, *171*(4), 339-358.

Gaston, A. J., Gilchrist, H. G., & Hipfner, J. M. (2005). Climate change, ice conditions and reproduction in an Arctic nesting marine bird: Brunnich's guillemot (*Uria lomvia* L.). *Journal of Animal Ecology*, *74*(5), 832-841.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*(6394), 1232-1235.

Germain, M., Pärt, T., Gustafsson, L., & Doligez, B. (2017). Natal dispersers pay a lifetime cost to increased reproductive effort in a wild bird population. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1851), 20162445.

Gibbs, H. K., Ruesch, A. S., Achard, F., Clayton, M. K., Holmgren, P., Ramankutty, N., & Foley, J. A. (2010). Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences*, *107*(38), 16732-16737.

Gienapp, P., & Merilä, J. (2011). Sex-specific fitness consequences of dispersal in Siberian jays. *Behavioral Ecology and Sociobiology*, *65*(2), 131-140.

Gienapp, P., Teplitsky, C., Alho, J. S., Mills, J. A., & Merilä, J. (2007). Climate change and evolution: disentangling environmental and genetic responses. *Molecular ecology*, *17*(1), 167-178.

Gilman, E. L. (2011). Bycatch governance and best practice mitigation technology in global tuna fisheries. *Marine Policy*, *35*(5), 590-609.

Glista, D. J., DeVault, T. L., & DeWoody, J. A. (2008). Vertebrate road mortality predominantly impacts amphibians. *Herpetological Conservation and Biology*, *3*(1), 77-87.

Goodwyn, P. P., & Fujisaki, K. (2007). Sexual conflicts, loss of flight, and fitness gains in locomotion of polymorphic water striders. *Entomologia experimentalis et applicata*, *124*(3), 249-259.

Goulson, D. (2014). Ecology: Pesticides linked to bird declines. *Nature*, *511*(7509), 295.

Green, R. J., & Higginbottom, K. (2000). The effects of non-consumptive wildlife tourism on free-ranging wildlife: a review. *Pacific conservation biology*, *6*(3), 183-197.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal behaviour*, *28*(4), 1140-1162.

Gros, A., Hovestadt, T., & Poethke, H. J. (2008). Evolution of sex-biased dispersal: the role of sex-specific dispersal costs, demographic stochasticity, and inbreeding. *Ecological Modelling*, *219*(1-2), 226-233.

Gross, M. R., Repka, J., Robertson, C. T., Secor, D. H., & Van Winkle, W. (2002). Sturgeon conservation: insights from elasticity analysis. In *American Fisheries Society Symposium* (Vol. 28, pp. 13-30).

Guerra, P. A. (2011). Evaluating the life-history trade-off between dispersal capability and reproduction in wing dimorphic insects: a meta-analysis. *Biological Reviews*, *86*(4), 813-835.

Gundersen, G., Johannesen, E., Andreassen, H. P., & Ims, R. A. (2001). Source–sink dynamics: how sinks affect demography of sources. Ecology Letters, 4(1), 14-21.

Gurnell, J., Lurz, P., & Bertoldi, W. (2014). The changing patterns in the distribution of red and grey squirrels in the North of England and Scotland between 1991 and 2010 based on volunteer surveys. *Hystrix, the Italian Journal of Mammalogy*, *25*(2), 83-89.

Gyllenberg, M., Kisdi, É., & Utz, M. (2008). Evolution of condition-dependent dispersal under kin competition. Journal of Mathematical Biology, 57(2), 285-307.

Hanski, I. (1998). Metapopulation dynamics. *Nature*, *396*(6706), 41.

Hanski, I., Erälahti, C., Kankare, M., Ovaskainen, O., & Sirén, H. (2004). Variation in migration propensity among individuals maintained by landscape structure. *Ecology letters*, *7*(10), 958-966.

Hansson, L. (1991). Dispersal and connectivity in metapopulations. *Biological journal of the Linnean Society*, *42*(1-2), 89-103.

Hansson, B., Bensch, S., & Hasselquist, D. (2004). Lifetime fitness of short-and long-distance dispersing great reed warblers. *Evolution*, *58*(11), 2546-2557.

Harley, C. D. (2011). Climate change, keystone predation, and biodiversity loss. *Science*, *334*(6059), 1124-1127.

Harris, C. M., Park, K. J., Atkinson, R., Edwards, C., & Travis, J. M. J. (2009). Invasive species control: incorporating demographic data and seed dispersal into a management model for *Rhododendron ponticum*. *Ecological Informatics*, *4*(4), 226-233.

Harwood, J. (2001). Marine mammals and their environment in the twenty-first century. Journal of Mammalogy, 82(3), 630-640.

Haughland, D. L., & Larsen, K. W. (2004). Exploration correlates with settlement: red squirrel dispersal in contrasting habitats. *Journal of Animal Ecology*, *73*(6), 1024-1034.

Hautier, Y., Tilman, D., Isbell, F., Seabloom, E. W., Borer, E. T., & Reich, P. B. (2015). Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, *348*(6232), 336-340.

Hawkes, C. (2009). Linking movement behaviour, dispersal and population processes: is individual variation a key?. *Journal of Animal Ecology*, *78*(5), 894-906.

Heino, M., & Hanski, I. (2001). Evolution of migration rate in a spatially realistic metapopulation model. *The American Naturalist*, *157*(5), 495-511.

Hendry, A. P., Farrugia, T. J., & Kinnison, M. T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Molecular ecology*, *17*(1), 20-29.

Henriques-Silva, R., Boivin, F., Calcagno, V., Urban, M. C., & Peres-Neto, P. R. (2015). On the evolution of dispersal via heterogeneity in spatial connectivity. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1803), 20142879.

Hereford, J. (2009). A quantitative survey of local adaptation and fitness trade-offs. *The American Naturalist*, *173*(5), 579-588.

Hewison, A. M., Morellet, N., Verheyden, H., Daufresne, T., Angibault, J. M., Cargnelutti, B., ... & Lourtet, B. (2009). Landscape fragmentation influences winter body mass of roe deer. *Ecography*, *32*(6), 1062-1070.

Hidalgo, J., De Casas, R. R., & Muñoz, M. Á. (2016). Environmental unpredictability and inbreeding depression select for mixed dispersal syndromes. *BMC evolutionary biology*, *16*(1), 71.

Hoegh-Guldberg, O., & Bruno, J. F. (2010). The impact of climate change on the world's marine ecosystems. *Science*, *328*(5985), 1523-1528.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., ... & Knowlton, N. (2007). Coral reefs under rapid climate change and ocean acidification. *science*, *318*(5857), 1737-1742.

Hogan, J. D., Blum, M. J., Gilliam, J. F., Bickford, N., & McIntyre, P. B. (2014). Consequences of alternative dispersal strategies in a putatively amphidromous fish. *Ecology*, *95*(9), 2397-2408.

Hooper, D. U., Adair, E. C., Cardinale, B. J., Byrnes, J. E., Hungate, B. A., Matulich, K. L., ... & O'Connor, M. I. (2012). A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature*, *486*(7401), 105.

Hothorn, T., Brandl, R., & Müller, J. (2012). Large-scale model-based assessment of deer-vehicle collision risk. *PLoS One*, 7(2), e29510.

Hovestadt, T., Messner, S., & Hans, J. P. (2001). Evolution of reduced dispersal mortality and 'fat-tailed'dispersal kernels in autocorrelated landscapes. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1465), 385-391.

Hovestadt, T., Bonte, D., Dytham, C., & Poethke, H. J. (2012). Evolution and emergence of dispersal kernels–a brief theoretical evaluation. *Dispersal ecology and evolution*, *211*, 221.

Ims, R. A., & Andreassen, H. P. (2000). Spatial synchronization of vole population dynamics by predatory birds. *Nature*, *408*(6809), 194.

IPCC, 2014: Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Isbell, L. A. & Van Vuren, D. (1996). Differential costs of locational and social dispersal and their consequences for female group-living primates. Behaviour, 133(1-2), 1-36.

Johnson, C. A., Fryxell, J. M., Thompson, I. D., & Baker, J. A. (2009). Mortality risk increases with natal dispersal distance in American martens. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1671), 3361-3367.

Jones, N. F., Pejchar, L., & Kiesecker, J. M. (2015). The energy footprint: how oil, natural gas, and wind energy affect land for biodiversity and the flow of ecosystem services. *BioScience*, *65*(3), 290-301.

Kahlenberg, S. M., Thompson, M. E., Muller, M. N., & Wrangham, R. W. (2008). Immigration costs for female chimpanzees and male protection as an immigrant counterstrategy to intrasexual aggression. Animal behaviour, 76(5), 1497-1509.

Kamp, J., Oppel, S., Ananin, A. A., Durnev, Y. A., Gashev, S. N., Hölzel, N., ... & Timonen, S. (2015). Global population collapse in a superabundant migratory bird and illegal trapping in China. *Conservation biology*, *29*(6), 1684-1694.

Karl, T. R., Melillo, J. M., Peterson, T. C., & Hassol, S. J. (Eds.). (2009). *Global climate change impacts in the United States*. Cambridge University Press.

Kasworm, W. F., & Manley, T. L. (1990). Road and trail influences on grizzly bears and black bears in northwest Montana. *Bears: their biology and management*, 79-84.

Kawecki, T. J. (2004). Ecological and evolutionary consequences of source-sink population dynamics. In Ecology, genetics and evolution of metapopulations (pp. 387-414). Academic Press.

Kingma, S. A., Komdeur, J., Hammers, M., & Richardson, D. S. (2016). The cost of prospecting for dispersal opportunities in a social bird. *Biology letters*, *12*(6), 20160316.

Klaus, S. P., & Lougheed, S. C. (2013). Changes in breeding phenology of eastern Ontario frogs over four decades. *Ecology and evolution*, *3*(4), 835-845.

Ko, J. Y., & Day, J. W. (2004). A review of ecological impacts of oil and gas development on coastal ecosystems in the Mississippi Delta. *Ocean & Coastal Management*, *47*(11-12), 597-623.

Koh, L. P., Dunn, R. R., Sodhi, N. S., Colwell, R. K., Proctor, H. C., & Smith, V. S. (2004). Species coextinctions and the biodiversity crisis. *science*, *305*(5690), 1632-1634.

Kokko, H., & López-Sepulcre, A. (2006). From individual dispersal to species ranges: perspectives for a changing world. *Science*, *313*(5788), 789-791.

Kramer-Schadt, S., Revilla, E., Wiegand, T., & Breitenmoser, U. R. S. (2004). Fragmented landscapes, road mortality and patch connectivity: modelling influences on the dispersal of Eurasian lynx. *Journal of Applied Ecology*, *41*(4), 711-723.

Kramer-Schadt, S., Kaiser, T. S., Frank, K., & Wiegand, T. (2011). Analyzing the effect of stepping stones on target patch colonisation in structured landscapes for Eurasian lynx. *Landscape ecology*, *26*(4), 501-513.

Krist, A. C., Jokela, J., Wiehn, J., & Lively, C. M. (2004). Effects of host condition on susceptibility to infection, parasite developmental rate, and parasite transmission in a snail–trematode interaction. Journal of Evolutionary Biology, 17(1), 33-40.

Kroodsma, D. A., Mayorga, J., Hochberg, T., Miller, N. A., Boerder, K., Ferretti, F., ... & Woods, P. (2018). Tracking the global footprint of fisheries. *Science*, *359*(6378), 904-908.

Kurihara, H. (2008). Effects of CO2-driven ocean acidification on the early developmental stages of invertebrates. *Marine Ecology Progress Series*, *373*, 275-284.

Kuparinen, A., Katul, G., Nathan, R., & Schurr, F. M. (2009). Increases in air temperature can promote wind-driven dispersal and spread of plants. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1670), 3081-3087.

Ladle, A., Steenweg, R., Shepherd, B., & Boyce, M. S. (2018). The role of human outdoor recreation in shaping patterns of grizzly bear-black bear co-occurrence. *PloS one*, *13*(2), e0191730.

Lambin, X., Le Bouille, D., Oliver, M. K., Sutherland, C., Tedesco, E., Douglas, A., ... & Bullock, J. M. (2012). High connectivity despite high fragmentation: iterated dispersal in a vertebrate metapopulation. *Dispersal ecology and evolution. Oxford University Press, Oxford*, 405-412.

Laurance, W. F. (2007). Have we overstated the tropical biodiversity crisis?. *Trends in Ecology & Evolution*, *22*(2), 65-70.

Laurance, W. F. (2010). Habitat destruction: death by a thousand cuts. *Conservation biology for all*, *1*(9), 73-88.

Lawson Handley, L. J., & Perrin, N. (2007). Advances in our understanding of mammalian sex-biased dispersal. *Molecular ecology*, *16*(8), 1559-1578.

Le Galliard, J. F., Massot, M., & Clobert, J. (2012). Dispersal and range dynamics in changing climates: a review. *Dispersal ecology and evolution. Oxford University Press, Oxford*, 317-336.

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., ... & Loreau, M. (2004). The metacommunity concept: a framework for multi-scale community ecology. *Ecology letters*, *7*(7), 601-613.

Lenarz, M. S., Nelson, M. E., Schrage, M. W., & Edwards, A. J. (2009). Temperature mediated moose survival in northeastern Minnesota. *The Journal of Wildlife Management*, *73*(4), 503-510.

Lenoir, J., Gégout, J. C., Marquet, P. A., De Ruffray, P., & Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *science*, *320*(5884), 1768-1771.

Lenormand, T. (2002). Gene flow and the limits to natural selection. Trends in Ecology & Evolution, 17(4), 183-189.

Leong, M., Ponisio, L. C., Kremen, C., Thorp, R. W., & Roderick, G. K. (2016). Temporal dynamics influenced by global change: bee community phenology in urban, agricultural, and natural landscapes. Global change biology, 22(3), 1046-1053.

Li, H., Aide, T. M., Ma, Y., Liu, W., & Cao, M. (2007). Demand for rubber is causing the loss of high diversity rain forest in SW China. In *Plant Conservation and Biodiversity* (pp. 157-171). Springer, Dordrecht.

Liberg, O., Johansson, A., Andersen, R., & Linnell, J. D. C. (1998). Mating system, mating tactics and the function of male territoriality in roe deer. *The European roe deer: the biology of success. Scandinavian University Press*, *Oslo*, 221-256.

Linnell, J. D., Brøseth, H., Solberg, E. J., & Brainerd, S. M. (2005). The origins of the southern Scandinavian wolf *Canis lupus* population: potential for natural immigration in relation to dispersal distances, geography and Baltic ice. *Wildlife Biology*, *11*(4), 383-392.

Liu, F., McShea, W. J., Garshelis, D. L., Zhu, X., Wang, D., & Shao, L. (2011). Human-wildlife conflicts influence attitudes but not necessarily behaviors: Factors driving the poaching of bears in China. *Biological Conservation*, *144*(1), 538-547.

Long, E. S., Diefenbach, D. R., Rosenberry, C. S., Wallingford, B. D., & Grund, M. D. (2005). Forest cover influences dispersal distance of white-tailed deer. *Journal of Mammalogy*, *86*(3), 623-629.

Longcore, T., & Rich, C. (2004). Ecological light pollution. *Frontiers in Ecology and the Environment*, *2*(4), 191-198.

Maag, N., Cozzi, G., Bateman, A., Heistermann, M., Ganswindt, A., Manser, M., ... & Ozgul, A. (2019). Cost of dispersal in a social mammal: body mass loss and increased stress. *Proceedings of the Royal Society B*, *286*(1896), 20190033.

Mandujano, S., Escobedo-Morales, L. A., & Palacios-Silva, R. (2004). Movements of *Alouatta palliata* among forest fragments in Los Tuxtlas, Mexico. *Neotropical Primates*, *12*(3), 126-132.

Martin, A. E., & Fahrig, L. (2015). Matrix quality and disturbance frequency drive evolution of species behavior at habitat boundaries. *Ecology and evolution*, *5*(24), 5792-5800.

Martin, J., Vourc'h, G., Bonnot, N., Cargnelutti, B., Chaval, Y., Lourtet, B., ... & Morellet, N. (2018). Temporal shifts in landscape connectivity for an ecosystem engineer, the roe deer, across a multiple-use landscape. *Landscape ecology*, *33*(6), 937-954.

Martínez-Mota, R., Valdespino, C., Sánchez-Ramos, M. A., & Serio-Silva, J. C. (2007). Effects of forest fragmentation on the physiological stress response of black howler monkeys. *Animal Conservation*, *10*(3), 374-379.

Marzluff, J. M. (2001). Worldwide urbanization and its effects on birds. In *Avian ecology and conservation in an urbanizing world* (pp. 19-47). Springer, Boston, MA.

Massemin, S., Maho, Y. L., & Handrich, Y. (1998). Seasonal pattern in age, sex and body condition of Barn Owls *Tyto alba* killed on motorways. *Ibis*, *140*(1), 70-75.

Massol, F., & Cheptou, P. O. (2010). Evolutionary syndromes linking dispersal and mating system: the effect of autocorrelation in pollination conditions. *Evolution: International Journal of Organic Evolution*, *65*(2), 591-598.

Massot, M., Clobert, J., Lorenzon, P., & Rossi, J. M. (2002). Condition-dependent dispersal and ontogeny of the dispersal behaviour: an experimental approach. *Journal of Animal Ecology*, *71*(2), 253-261.

Massot, M., Clobert, J., & FerriERe, R. (2008). Climate warming, dispersal inhibition and extinction risk. *Global Change Biology*, *14*(3), 461-469.

Mathias, A., Kisdi, È., & Olivieri, I. (2001). Divergent evolution of dispersal in a heterogeneous landscape. *Evolution*, *55*(2), 246-259.

Mathieu, J., Barot, S., Blouin, M., Caro, G., Decaëns, T., Dubs, F., ... & Nai, P. (2010). Habitat quality, conspecific density, and habitat pre-use affect the dispersal behaviour of two earthworm species, *Aporrectodea icterica* and *Dendrobaena veneta*, in a mesocosm experiment. *Soil Biology and Biochemistry*, *42*(2), 203-209.

Matthysen, E. (2012). Multicausality of dispersal: a review. *Dispersal ecology and evolution*, *27*, 3-18.

Mayer, M., Zedrosser, A., & Rosell, F. (2017). When to leave: the timing of natal dispersal in a large, monogamous rodent, the Eurasian beaver. *Animal Behaviour*, *123*, 375-382.

McKinney, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological conservation*, *127*(3), 247-260.

McKinney, M. L. (2008). Effects of urbanization on species richness: a review of plants and animals. *Urban ecosystems*, *11*(2), 161-176.

McLay, L. K., Green, M. P., & Jones, T. M. (2017). Chronic exposure to dim artificial light at night decreases fecundity and adult survival in *Drosophila melanogaster*. Journal of insect physiology, 100, 15-20.

McLellan, B. N., & Hovey, F. W. (2001). Natal dispersal of grizzly bears. *Canadian Journal of Zoology*, *79*(5), 838-844.

Mech, S. G., & Hallett, J. G. (2001). Evaluating the effectiveness of corridors: a genetic approach. *Conservation Biology*, *15*(2), 467-474.

Medina, F. M., Bonnaud, E., Vidal, E., Tershy, B. R., Zavaleta, E. S., Josh Donlan, C., ... & Nogales, M. (2011). A global review of the impacts of invasive cats on island endangered vertebrates. *Global Change Biology*, *17*(11), 3503-3510.

Mennechez, G., Petit, S., Schtickzelle, N., & Baguette, M. (2004). Modelling mortality and dispersal: consequences of parameter generalisation on metapopulation dynamics. *Oikos*, *106*(2), 243-252.

Milazzo, M., Chemello, R., Badalamenti, F., Camarda, R., & Riggio, S. (2002). The impact of human recreational activities in marine protected areas: what lessons should be learnt in the Mediterranean sea?. *Marine ecology*, *23*, 280-290.

Milly, P. C. D., Wetherald, R. T., Dunne, K. A., & Delworth, T. L. (2002). Increasing risk of great floods in a changing climate. *Nature*, *415*(6871), 514.

Mitchum, G., Dutton, A., Chambers, D. P., & Wdowinski, S. (2017). Sea Level Rise. *Florida's Climate: Changes, Variations, & Impacts*.

Møller, A. P., Flensted-Jensen, E., & Mardal, W. (2006). Dispersal and climate change: a case study of the Arctic tern *Sterna paradisaea*. *Global Change Biology*, *12*(10), 2005-2013.

Mooney, H. A., & Hobbs, R. J. (2000). Global change and invasive species: where do we go from here. *Invasive species in a changing world. Island Press, Washington, DC*, 425-434.

Mousseau, T. A., & Fox, C. W. (1998). The adaptive significance of maternal effects. *Trends in ecology & evolution*, *13*(10), 403-407.

Murray, D. L., Cox, E. W., Ballard, W. B., Whitlaw, H. A., Lenarz, M. S., Custer, T. W., ... & Fuller, T. K. (2006). Pathogens, nutritional deficiency, and climate influences on a declining moose population. Wildlife Monographs, 166(1), 1-30.

Murren, C. J., Auld, J. R., Callahan, H., Ghalambor, C. K., Handelsman, C. A., Heskel, M. A., ... & Pfennig, D. W. (2015). Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. Heredity, 115(4), 293.

Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052-19059.

Nathan, R., Klein, E. K., Robledo-Arnuncio, J. J., & Revilla, E. (2012). Dispersal kernels. In *Dispersal ecology and evolution* (pp. 187-210). Oxford: Oxford University Press.

Nevoux, M., Arlt, D., Nicoll, M., Jones, C., & Norris, K. (2013). The short-and long-term fitness consequences of natal dispersal in a wild bird population. *Ecology letters*, *16*(4), 438-445.

Newman, J. R. (1979). Effects of industrial air pollution on wildlife. *Biological conservation*, 15(3), 181-190.

Newman, J. R., & Schreiber, R. K. (1988). Air pollution and wildlife toxicology: An overlooked problem. *Environmental Toxicology and Chemistry: An International Journal*, 7(5), 381-390.

Nicolaus, M., Tinbergen, J. M., Bouwman, K. M., Michler, S. P., Ubels, R., Both, C., ... & Dingemanse, N. J. (2012). Experimental evidence for adaptive personalities in a wild passerine bird. *Proceedings of the Royal Society B: Biological Sciences*, 279(1749), 4885-4892.

Nunes, S., & Holekamp, K. E. (1996). Mass and fat influence the timing of natal dispersal in Belding's ground squirrels. *Journal of Mammalogy*, 77(3), 807-817.

Nussey, D. H., Postma, E., Gienapp, P., & Visser, M. E. (2005). Selection on heritable phenotypic plasticity in a wild bird population. *Science*, 310(5746), 304-306.

North, A., Cornell, S., & Ovaskainen, O. (2011). Evolutionary responses of dispersal distance to landscape structure and habitat loss. *Evolution: International Journal of Organic Evolution*, *65*(6), 1739-1751.

O'Connell, L. M., Mosseler, A., & Rajora, O. P. (2007). Extensive long-distance pollen dispersal in a fragmented landscape maintains genetic diversity in white spruce. *Journal of heredity*, 98(7), 640-645.

Olden, J. D., Schooley, R. L., Monroe, J. B., & Poff, N. L. (2004). Context-dependent perceptual ranges and their relevance to animal movements in landscapes. *Journal of Animal Ecology*, *73*(6), 1190-1194.

Ollerton, J., Erenler, H., Edwards, M., & Crockett, R. (2014). Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science*, *346*(6215), 1360-1362.

Paetzold, A., Smith, M., Warren, P. H., & Maltby, L. (2011). Environmental impact propagated by cross-system subsidy: Chronic stream pollution controls riparian spider populations. *Ecology*, *92*(9), 1711-1716.

Pakanen, V. M., Koivula, K., Orell, M., Rytkönen, S., & Lahti, K. (2016). Sex-specific mortality costs of dispersal during the post-settlement stage promote male philopatry in a resident passerine. *Behavioral ecology and sociobiology*, *70*(10), 1727-1733.

Pardini, A. T., Jones, C. S., Noble, L. R., Kreiser, B., Malcolm, H., Bruce, B. D., ... & Duffy, C. A. (2001). Sex-biased dispersal of great white sharks. *Nature*, *412*(6843), 139.

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., ... & Tennent, W. J. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, *399*(6736), 579.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, *37*, 637-669.

Pärn, H., Jensen, H., Ringsby, T. H., & Sæther, B. E. (2009). Sex-specific fitness correlates of dispersal in a house sparrow metapopulation. *Journal of Animal Ecology*, *78*(6), 1216-1225.

Parvinen, K. (2005). Evolutionary suicide. *Acta biotheoretica*, 53(3), 241-264.

Pe'er, G., & Kramer-Schadt, S. (2008). Incorporating the perceptual range of animals into connectivity models. *Ecological Modelling*, *213*(1), 73-85.

Pellerin, M., Bessière, A., Maillard, D., Capron, G., Gaillard, J. M., Michallet, J., & Bonenfant, C. (2017). Saving time and money by using diurnal vehicle counts to monitor roe deer abundance. Wildlife Biology, 2017(4).

Pérez-González, J., & Carranza, J. (2009). Female-biased dispersal under conditions of low male mating competition in a polygynous mammal. *Molecular ecology*, *18*(22), 4617-4630.

Péron, G., Crochet, P. A., Choquet, R., Pradel, R., Lebreton, J. D., & Gimenez, O. (2010). Capture–recapture models with heterogeneity to study survival senescence in the wild. *Oikos*, 119(3), 524-532.

Perrin, N., & Mazalov, V. (2000). Local competition, inbreeding, and the evolution of sex-biased dispersal. *The American Naturalist*, *155*(1), 116-127.

Parvinen, K. (2005). Evolutionary suicide. *Acta biotheoretica*, *53*(3), 241-264.

Pelini, S. L., Prior, K. M., Parker, D. J., Dzurisin, J. D., Lindroth, R. L., & Hellmann, J. J. (2009). Climate change and temporal and spatial mismatches in insect communities. In *Climate Change* (pp. 215-231). Elsevier.

Pettorelli, N., Gaillard, J. M., Duncan, P., Ouellet, J. P., & Van Laere, G. (2001). Population density and small-scale variation in habitat quality affect phenotypic quality in roe deer. *Oecologia*, 128(3), 400-405.

Phillips, B. L., Brown, G. P., & Shine, R. (2010). Life-history evolution in range-shifting populations. *Ecology*, *91*(6), 1617-1627.

Pimm, S. L., & Raven, P. (2000). Biodiversity: extinction by numbers. *Nature*, *403*(6772), 843.

Planes, S., Jones, G. P., & Thorrold, S. R. (2009). Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Sciences*, *106*(14), 5693-5697.

Polidoro, B. A., Carpenter, K. E., Collins, L., Duke, N. C., Ellison, A. M., Ellison, J. C., ... & Livingstone, S. R. (2010). The loss of species: mangrove extinction risk and geographic areas of global concern. *PloS one*, 5(4), e10095.

Ponchon, A., Garnier, R., Grémillet, D., & Boulinier, T. (2015a). Predicting population responses to environmental change: the importance of considering informed dispersal strategies in spatially structured population models. *Diversity and Distributions*, *21*(1), 88-100.

Ponchon, A., Chambert, T., Lobato, E., Tveraa, T., Grémillet, D., & Boulinier, T. (2015b). Breeding failure induces large scale prospecting movements in the black-legged kittiwake. *Journal of Experimental Marine Biology and Ecology*, *473*, 138-145.

Pringle, C. M. (2001). Hydrologic connectivity and the management of biological reserves: a global perspective. *Ecological Applications*, 11(4), 981-998.

Pulido, F., & Berthold, P. (2004). Microevolutionary response to climatic change. *Advances in Ecological Research*, *35*, 151-183.

Purcell, J., Brelsford, A., & Avilés, L. (2012). Co-evolution between sociality and dispersal: the role of synergistic cooperative benefits. *Journal of theoretical biology*, *312*, 44-54.

Ramankutty, N., & Foley, J. A. (1998). Characterizing patterns of global land use: An analysis of global croplands data. *Global Biogeochemical Cycles*, *12*(4), 667-685.

Rand, A. S., Bridarolli, M. E., Dries, L., & Ryan, M. J. (1997). Light levels influence female choice in túngara frogs: predation risk assessment?. *Copeia*, 447-450.

Réale, D., McAdam, A. G., Boutin, S., & Berteaux, D. (2003). Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1515), 591-596.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., & Montiglio, P. O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1560), 4051-4063.

Rehage, J. S., Cote, J., & Sih, A. (2016). The role of dispersal behaviour and personality in post-establishment spread. *Biological Invasions and Animal Behaviour*, 96-116.

Rémy, A., Le Galliard, J. F., Odden, M., & Andreassen, H. P. (2013). Concurrent effects of age class and food distribution on immigration success and population dynamics in a small mammal. *journal of animal ecology*, *83*(4), 813-822.

Reynolds, J., & Peres, C. A. (2006). Overexploitation. In: Principles of Conservation Biology. Sinauer, Sunderland, Mass, pp. 249-287

Rhein, M., Rintoul, S.R., Aoki, S., Campos, E., Chambers, D., Feely, R.A., Gulev, S., Johnson, G.C., Josey, S.A., Kostianoy, A., Mauritzen, C., Roemmich, D. and Talley, L.D. (2013) Observations: Ocean. In, Stocker, T.F., Qin, D., Plattner, G.-K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. and Midgley, P.M. (eds.) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge, GB. Cambridge University Press, pp. 255-316.

Richards, J. F. (1990). Land transformation. *The earth as transformed by human action*, 163-178.

Richardson, J. L., Brady, S. P., Wang, I. J., & Spear, S. F. (2016). Navigating the pitfalls and promise of landscape genetics. *Molecular Ecology*, *25*(4), 849-863.

Ridley, A. R., Raihani, N. J., & Nelson-Flower, M. J. (2008). The cost of being alone: the fate of floaters in a population of cooperatively breeding pied babblers *Turdoides bicolor*. *Journal of Avian Biology*, 39(4), 389-392.

Rieman, B., Lee, D., McIntyre, J., Overton, K., & Thurow, R. (1993). Consideration of extinction risks for salmonids. *Fish habitat relationships technical bulletin*, 14, 12.

Ritchie, H. and Roser, M. (2019) - "Urbanization". *Published online at OurWorldInData.org.* Retrieved from: 'https://ourworldindata.org/urbanization' [Online Resource]

Robertson, B. A., & Chalfoun, A. D. (2016). Evolutionary traps as keys to understanding behavioral maladapation. *Current Opinion in Behavioral Sciences*, *12*, 12-17.

Robinson, L. M., Hobday, A. J., Possingham, H. P., & Richardson, A. J. (2015). Trailing edges projected to move faster than leading edges for large pelagic fish habitats under climate change. *Deep Sea Research Part II: Topical Studies in Oceanography*, 113, 225-234.

Ronce, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annu. Rev. Ecol. Evol. Syst.*, *38*, 231-253.

Ronce, O., & Clobert, J. (2012). Dispersal syndromes. *Dispersal ecology and evolution*, *155*, 119-138.

Ronce, O., Clobert, J., & Massot, M. (1998). Natal dispersal and senescence. *Proceedings of the National Academy of Sciences*, *95*(2), 600-605.

Roper, T. J., Ostler, J. R., & Conradt, L. (2003). The process of dispersal in badgers *Meles meles*. *Mammal Review*, *33*(3-4), 314-318.

Rosenberg, A. A. (2003). Managing to the margins: the overexploitation of fisheries. *Frontiers in Ecology and the Environment*, *1*(2), 102-106.

Roze, D., & Rousset, F. (2003). Selection and drift in subdivided populations: a straightforward method for deriving diffusion approximations and applications involving dominance, selfing and local extinctions. *Genetics*, *165*(4), 2153-2166.

Roze, D., & Rousset, F. (2005). Inbreeding depression and the evolution of dispersal rates: a multilocus model. *The American Naturalist*, *166*(6), 708-721.

Russell, A. F. (2001). Dispersal costs set the scene for helping in an atypical avian cooperative breeder. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1462), 95-99.

Saastamoinen, M., Bocedi, G., Cote, J., Legrand, D., Guillaume, F., Wheat, C. W., ... & Baguette, M. (2018). Genetics of dispersal. *Biological Reviews*, *93*(1), 574-599.

Sæther, B. E., & Bakke, Ø. (2000). Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology*, *81*(3), 642-653.

Saccheri, I., Kuussaari, M., Kankare, M., Vikman, P., Fortelius, W., & Hanski, I. (1998). Inbreeding and extinction in a butterfly metapopulation. *Nature*, 392(6675), 491.

Sage, R. B., Hollins, K., Gregory, C. L., Woodburn, M. I., & Carroll, J. P. (2004). Impact of roe deer *Capreolus capreolus* browsing on understorey vegetation in small farm woodlands. *Wildlife biology*, 10(1), 115-121.

Sakakura, Y., & Tsukamoto, K. (1998). Effects of density, starvation and size difference on aggressive behaviour in juvenile yellowtails (*Seriola quinquevadiata*). *Journal of Applied Ichthyology*, *14*(1-2), 9-13.

Sarno, R. J., Bank, M. S., Stern, H. S., & Franklin, W. L. (2003). Forced dispersal of juvenile guanacos (*Lama guanicoe*): causes, variation, and fates of individuals dispersing at different times. *Behavioral Ecology and Sociobiology*, *54*(1), 22-29.

Saura, S., Bodin, Ö., & Fortin, M. J. (2014). EDITOR'S CHOICE: Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, *51*(1), 171-182.

Sawyer, H., LeBeau, C. W., McDonald, T. L., Xu, W., & Middleton, A. D. All routes are not created equal: an ungulate's choice of migration route can influence its survival. *Journal of Applied Ecology*.

Schloss, C. A., Nuñez, T. A., & Lawler, J. J. (2012). Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. *Proceedings of the National Academy of Sciences*, 109(22), 8606-8611.

Schtickzelle, N., Mennechez, G., & Baguette, M. (2006). Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology*, *87*(4), 1057-1065.

Schweiger, O., Settele, J., Kudrna, O., Klotz, S., & Kühn, I. (2008). Climate change can cause spatial mismatch of trophically interacting species. *Ecology*, *89*(12), 3472-3479.

Schweiger, O., Heikkinen, R. K., Harpke, A., Hickler, T., Klotz, S., Kudrna, O., ... & Settele, J. (2012). Increasing range mismatching of interacting species under global change is related to their ecological characteristics. *Global Ecology and Biogeography*, *21*(1), 88-99.

Scrafford, M. A., Avgar, T., Abercrombie, B., Tigner, J., & Boyce, M. S. (2017). Wolverine habitat selection in response to anthropogenic disturbance in the western Canadian boreal forest. *Forest ecology and management*, *395*, 27-36.

Seabrook, L., McAlpine, C., Baxter, G., Rhodes, J., Bradley, A., & Lunney, D. (2011). Drought-driven change in wildlife distribution and numbers: a case study of koalas in south west Queensland. *Wildlife Research*, *38*(6), 509-524.

Searcy, C. A., Gilbert, B., Krkošek, M., Rowe, L., & McCauley, S. J. (2018). Positive correlation between dispersal and body size in Green Frogs (*Rana clamitans*) naturally colonizing an experimental landscape. *Canadian Journal of Zoology*, 96(12), 1378-1384.

Selonen, V., & Hanski, I. K. (2009). Decision making in dispersing Siberian flying squirrels. *Behavioral Ecology*, 21(2), 219-225.

Senior, R. A., Hill, J. K., & Edwards, D. P. (2019). Global loss of climate connectivity in tropical forests. *Nature Climate Change*, 9(8), 623-626.

Sheth, S. N., & Angert, A. L. (2018). Demographic compensation does not rescue populations at a trailing range edge. *Proceedings of the National Academy of Sciences*, 115(10), 2413-2418.

Shinya, M., Tsuchinaga, T., Kitano, M., Yamada, Y., & Ishikawa, M. (2000). Characterization of heavy metals and polycyclic aromatic hydrocarbons in urban highway runoff. *Water Science and Technology*, *42*(7-8), 201-208.

Sih, A., Bell, A., & Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in ecology & evolution*, *19*(7), 372-378.

Sih, A., Ferrari, M. C., & Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary applications*, *4*(2), 367-387.

Silverin, B. (1997). The stress response and autumn dispersal behaviour in willow tits. *Animal Behaviour*, *53*(3), 451-459.

Sim, I. M., Rebecca, G. W., Ludwig, S. C., Grant, M. C., & Reid, J. M. (2011). Characterizing demographic variation and contributions to population growth rate in a declining population. *Journal of Animal Ecology*, *80*(1), 159-170.

Simberloff, D., Farr, J. A., Cox, J., & Mehlman, D. W. (1992). Movement corridors: conservation bargains or poor investments?. *Conservation biology*, *6*(4), 493-504.

Simberloff, D. (2010). Invasive species. *Conservation biology for all*, 131-152. Oxford University Press.

Singh, N. J., Börger, L., Dettki, H., Bunnefeld, N., & Ericsson, G. (2012). From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. *Ecological Applications*, 22(7), 2007-2020.

Smith, A. T. (1987). Population structure of pikas: dispersal versus philopatry. *Mammalian dispersal patterns: the effects of social structure on population genetics (BD Chepko-Sade and ZT Halpin, eds.). University of Chicago Press, Chicago, Illinois*, 128-142.

Sinervo, B., Calsbeek, R., Comendant, T., Both, C., Adamopoulou, C., & Clobert, J. (2006). Genetic and maternal determinants of effective dispersal: the effect of sire genotype and size at birth in side-blotched lizards. *The American Naturalist*, *168*(1), 88-99.

E. Smith, J., & O. Batzli, G. (2006). Dispersal and mortality of prairie voles (*Microtus ochrogaster*) in fragmented landscapes: a field experiment. *Oikos*, *112*(1), 209-217.

Smith, J. A., Wang, Y., & Wilmers, C. C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1802), 20142711.

Solomon, N. G. (2003). A reexamination of factors influencing philopatry in rodents. *Journal of Mammalogy*, *84*(4), 1182-1197.

Soulsbury, C. D., Baker, P. J., Iossa, G., & Harris, S. (2008). Fitness costs of dispersal in red foxes (*Vulpes vulpes*). *Behavioral Ecology and Sociobiology*, *62*(8), 1289-1298.

Spaan, R. S., Epps, C. W., Ezenwa, V. O., & Jolles, A. E. (2019). Why did the buffalo cross the park? Resource shortages, but not infections, drive dispersal in female African buffalo (*Syncerus caffer*). *Ecology and evolution*, *9*(10), 5651-5663.

Spielman, D., Brook, B. W., & Frankham, R. (2004). Most species are not driven to extinction before genetic factors impact them. *Proceedings of the National Academy of Sciences*, *101*(42), 15261-15264.

Stamps, J. A. (2006). The silver spoon effect and habitat selection by natal dispersers. *Ecology Letters*, *9*(11), 1179-1185.

Stamps, J. A., Krishnan, V. V., & Reid, M. L. (2005). Search costs and habitat selection by dispersers. *Ecology*, *86*(2), 510-518.

Stephens, P. A., Sutherland, W. J., & Freckleton, R. P. (1999). What is the Allee effect?. *Oikos*, 185-190.

Sterck, E. H. (1998). Female dispersal, social organization, and infanticide in langurs: are they linked to human disturbance?. *American Journal of Primatology*, *44*(4), 235-254.

Stevens, V. M., Whitmee, S., Le Galliard, J. F., Clobert, J., Böhning-Gaese, K., Bonte, D., ... & Baguette, M. (2014). A comparative analysis of dispersal syndromes in terrestrial and semi-terrestrial animals. *Ecology letters*, *17*(8), 1039-1052.

Stroeve, J. C., Markus, T., Boisvert, L., Miller, J., & Barrett, A. (2014). Changes in Arctic melt season and implications for sea ice loss. *Geophysical Research Letters*, *41*(4), 1216-1225.

Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S., Fischman, D. L., & Waller, R. W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science*, 306(5702), 1783-1786.

Sunday, J. M., Bates, A. E., & Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of animals. *Nature Climate Change*, *2*(9), 686.

Taylor, P. D., Fahrig, L., Henein, K., & Merriam, G. (1993). Connectivity is a vital element of landscape structure. *Oikos*, 571-573.

Taylor, T. B., & Buckling, A. (2010). Competition and dispersal in *Pseudomonas aeruginosa*. *The American Naturalist*, 176(1), 83-89.

Taylor, B. D., & Goldingay, R. L. (2010). Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia. *Wildlife Research*, *37*(4), 320-331.

Teller, B. J., Miller, A. D., & Shea, K. (2015). Conservation of passively dispersed organisms in the context of habitat degradation and destruction. *Journal of applied ecology*, *52*(2), 514-521.

Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... & Hughes, L. (2004). Extinction risk from climate change. *Nature*, *427*(6970), 145.

Tischendorf, L., Bender, D. J., & Fahrig, L. (2003). Evaluation of patch isolation metrics in mosaic landscapes for specialist vs. generalist dispersers. *Landscape Ecology*, *18*(1), 41-50.

Torrents-Ticó, M., Bennett, N. C., Jarvis, J. U., & Zöttl, M. (2018). Growth affects dispersal success in social mole-rats, but not the duration of philopatry. *Biology letters*, 14(2), 20180005.

Traill, L. W., Lim, M. L., Sodhi, N. S., & Bradshaw, C. J. (2010). Mechanisms driving change: altered species interactions and ecosystem function through global warming. *Journal of Animal Ecology*, *79*(5), 937-947.

Trakhtenbrot, A., Nathan, R., Perry, G., & Richardson, D. M. (2005). The importance of long-distance dispersal in biodiversity conservation. *Diversity and Distributions*, *11*(2), 173-181.

Trapp, S. E., Day, C. C., Flaherty, E. A., Zollner, P. A., & Smith, W. P. (2019). Modeling impacts of landscape connectivity on dispersal movements of northern flying squirrels (*Glaucomys sabrinus griseifrons*). *Ecological modelling*, *394*, 44-52.

Tratalos, J. A., & Austin, T. J. (2001). Impacts of recreational SCUBA diving on coral communities of the Caribbean island of Grand Cayman. *Biological Conservation*, *102*(1), 67-75.

Travis, J. M., & Dytham, C. (1999). Habitat persistence, habitat availability and the evolution of dispersal. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1420), 723-728.

Travis, J. M., & Dytham, C. (2012). Dispersal and climate change: a review of theory. *Dispersal ecology and evolution*, 337-348.

Travis, J. M., Murrell, D. J., & Dytham, C. (1999). The evolution of density–dependent dispersal. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*(1431), 1837-1842.

Travis, J. M. (2001). The color of noise and the evolution of dispersal. *Ecological Research*, *16*(1), 157-163.

Travis, J. M. J. (2003). Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1514), 467-473.

Travis, J. M., & Dytham, C. (2012). Dispersal and climate change: a review of theory. *Dispersal ecology and evolution*, 337-348.

Travis, J. M., Mustin, K., Bartoń, K. A., Benton, T. G., Clobert, J., Delgado, M. M., ... & Bonte, D. (2012). Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. *Methods in Ecology and Evolution*, *3*(4), 628-641.

Travis, J. M., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., ... & Saastamoinen, M. (2013). Dispersal and species' responses to climate change. *Oikos*, *122*(11), 1532-1540.

Truvé, J., & Lemel, J. (2003). Timing and distance of natal dispersal for wild boar *Sus scrofa* in Sweden. *Wildlife Biology*, 9(4), 51-58.

Tucker, S., Mark Hipfner, J., & Trudel, M. (2016). Size-and condition-dependent predation: a seabird disproportionately targets substandard individual juvenile salmon. *Ecology*, 97(2), 461-471.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., ... & Bartlam-Brooks, H. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*(6374), 466-469.

Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology letters*, *11*(12), 1351-1363.

Václavík, T., & Meentemeyer, R. K. (2009). Invasive species distribution modeling (iSDM): Are absence data and dispersal constraints needed to predict actual distributions?. *Ecological modelling*, *220*(23), 3248-3258.

Valeix, M., Loveridge, A. J., Davidson, Z., Madzikanda, H., Fritz, H., & Macdonald, D. W. (2010). How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. *Landscape Ecology*, 25(3), 337-351.

Van Asch, M., Julkunen-Tiito, R., & Visser, M. E. (2010). Maternal effects in an insect herbivore as a mechanism to adapt to host plant phenology. *Functional Ecology*, *24*(5), 1103-1109.

Van Hezewijk, B., Wertman, D., Stewart, D., Béliveau, C., & Cusson, M. (2018). Environmental and genetic influences on the dispersal propensity of spruce budworm (*Choristoneura fumiferana*). *Agricultural and forest entomology*, *20*(3), 433-441.

Van Houtan, K. S., Pimm, S. L., Halley, J. M., Bierregaard Jr, R. O., & Lovejoy, T. E. (2007). Dispersal of Amazonian birds in continuous and fragmented forest. *Ecology letters*, 10(3), 219-229.

Van Moorter, B., Gaillard, J. M., Hewison, A. J. M., Said, S., Coulon, A., Delorme, D., ... & Cargnelutti, B. (2008). Evidence for exploration behaviour in young roe deer (*Capreolus capreolus*) prior to dispersal. *Ethology Ecology & Evolution*, 20(1), 1-15.

Van Oort, H. V., & Otter, K. A. (2005). Natal nutrition and the habitat distributions of male and female black-capped chickadees. *Canadian Journal of Zoology*, 83(11), 1495-1501.

Vanpé, C., Debeffe, L., Galan, M., Hewison, A. M., Gaillard, J. M., Gilot-Fromont, E., ... & Merlet, J. (2016). Immune gene variability influences roe deer natal dispersal. *Oikos*, 125(12), 1790-1801.

Vegter, A. C., Barletta, M., Beck, C., Borrero, J., Burton, H., Campbell, M. L., ... & Gilardi, K. V. (2014). Global research priorities to mitigate plastic pollution impacts on marine wildlife. *Endangered Species Research*, *25*(3), 225-247.

Vehmaa, A., Brutemark, A., & Engström-Öst, J. (2012). Maternal effects may act as an adaptation mechanism for copepods facing pH and temperature changes. *PLoS one*, *7*(10), e48538.

Visser, M. E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1635), 649-659.

Visser, M. E., & Holleman, L. J. (2001). Warmer springs disrupt the synchrony of oak and winter moth phenology. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1464), 289-294.

Visser, M. E., & Both, C. (2005). Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2561-2569.

Visser, M. E., te Marvelde, L., & Lof, M. E. (2012). Adaptive phenological mismatches of birds and their food in a warming world. *Journal of Ornithology*, 153(1), 75-84.

Vitousek, P. M., Mooney, H. A., Lubchenco, J., & Melillo, J. M. (1997). Human domination of Earth's ecosystems. *Science*, *277*(5325), 494-499.

Vitousek, P. M., Loope, L. L., & Westbrooks, R. (2017). Biological invasions as global environmental change.

Vor, T., Kiffner, C., Hagedorn, P., Niedrig, M., & Rühe, F. (2010). Tick burden on European roe deer (*Capreolus capreolus*). *Experimental and Applied Acarology*, 51(4), 405-417.

Wahlström, L. K., & Liberg, O. (1995). Patterns of dispersal and seasonal migration in roe deer (*Capreolus capreolus*). *Journal of Zoology*, 235(3), 455-467.

Walther, G. R. (2010). Community and ecosystem responses to recent climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2019-2024.

Wang and Peng 2001 Xiao-ping, Z. S. Q. Z. (2001). On heavy metal pollution along Yangtze river stretches of urban areas in major cities [J]. *Yangtze River*, *7*.

Wang, B. C., Sork, V. L., Leong, M. T., & Smith, T. B. (2007). Hunting of mammals reduces seed removal and dispersal of the afrotropical tree *Antrocaryon klaineanum* (Anacardiaceae). *Biotropica*, *39*(3), 340-347.

Ward, M. P. (2005). Habitat selection by dispersing yellow-headed blackbirds: evidence of prospecting and the use of public information. *Oecologia*, *145*(4), 650-657.

Warren, M. S., Hill, J. K., Thomas, J. A., Asher, J., Fox, R., Huntley, B., ... & Jeffcoate, G. (2001). Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature*, *414*(6859), 65.

Weimerskirch, H., Prudor, A., & Schull, Q. (2018). Flights of drones over sub-Antarctic seabirds show species-and status-specific behavioural and physiological responses. *Polar Biology*, *41*(2), 259-266.

Wilcox, C., Van Sebille, E., & Hardesty, B. D. (2015). Threat of plastic pollution to seabirds is global, pervasive, and increasing. *Proceedings of the National Academy of Sciences*, *112*(38), 11899-11904.

Wildy, E. L., Chivers, D. P., Kiesecker, J. M., & Blaustein, A. R. (2001). The effects of food level and conspecific density on biting and cannibalism in larval long-toed salamanders, *Ambystoma macrodactylum*. *Oecologia*, *128*(2), 202-209.

Wilson, A. J., & Nussey, D. H. (2010). What is individual quality? An evolutionary perspective. *Trends in Ecology & Evolution*, *25*(4), 207-214.

Wotton, D. M., & Kelly, D. (2012). Do larger frugivores move seeds further? Body size, seed dispersal distance, and a case study of a large, sedentary pigeon. *Journal of Biogeography*, 39(11), 1973-1983.

Winchell, K. M., Reynolds, R. G., Prado-Irwin, S. R., Puente-Rolón, A. R., & Revell, L. J. (2016). Phenotypic shifts in urban areas in the tropical lizard *Anolis cristatellus*. *Evolution*, *70*(5), 1009-1022.

Wingfield, J. C. (2008). Comparative endocrinology, environment and global change. *General and comparative endocrinology*, *157*(3), 207-216.

Wingfield, J. C. (2015). Coping with change: a framework for environmental signals and how neuroendocrine pathways might respond. *Frontiers in neuroendocrinology*, *37*, 89-96.

Wolf, J. B., & Wade, M. J. (2009). What are maternal effects (and what are they not)?. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1520), 1107-1115.

Woodroffe, R. (2000, May). Predators and people: using human densities to interpret declines of large carnivores. In *Animal Conservation Forum* (Vol. 3, No. 2, pp. 165-173). Cambridge University Press.

Wotton, D. M., & Kelly, D. (2012). Do larger frugivores move seeds further? Body size, seed dispersal distance, and a case study of a large, sedentary pigeon. *Journal of Biogeography*, 39(11), 1973-1983.

Yang, D., Song, Y., Ma, J., Li, P., Zhang, H., Price, M. R. S., ... & Jiang, Z. (2016). Stepping-stones and dispersal flow: establishment of a meta-population of Milu (*Elaphurus davidianus*) through natural re-wilding. *Scientific reports*, *6*, 27297.

Yasué, M., & Dearden, P. (2006). The potential impact of tourism development on habitat availability and productivity of Malaysian plovers *Charadrius peronii*. *Journal of Applied Ecology*, 43(5), 978-989.

Yoder, J. M., Marschall, E. A., & Swanson, D. A. (2004). The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behavioral Ecology*, *15*(3), 469-476.

Zera, A. J., & Brisson, J. A. (2012). Quantitative, physiological, and molecular genetics of dispersal/migration. *Dispersal ecology and evolution*, 63-82.

Zollner, P. A., & Lima, S. L. (1999). Search strategies for landscape-level interpatch movements. *Ecology*, *80*(3), 1019-1030.

Zollner, P. A. (2000). Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landscape ecology*, *15*(6), 523-533.

Résumé:

La dispersion natale est un processus durant lequel les individus se déplacent de leur domaine natal vers leur domaine de reproduction. Ce processus fondamental pour la dynamique et la persistance des populations passe par l'évitement de la consanguinité ou la capacité des individus à atteindre et coloniser de nouveaux habitats contenant des ressources ou des partenaires sexuels. La dispersion peut donc comporter de nombreux bénéfices pour les individus disperseurs. Cependant, elle peut également être coûteuse pour les individus, en raison d'une augmentation de la mortalité ou des blessures, une dépense énergétique élevée, ou enfin la perte d'un habitat natal favorable ou de temps à allouer à une autre activité. L'expression du phénotype de dispersion au niveau populationnel dépend donc de la balance entre coûts et bénéfices, et la théorie prévoit que les disperseurs devraient être contre-sélectionnés si les coûts deviennent supérieurs aux bénéfices engendrés par la dispersion. Dans le contexte actuel de changements globaux, on peut s'attendre à ce que (1) les coûts de la dispersion augmentent avec la dégradation de l'environnement et (2) à ce que cette augmentation des coûts de la dispersion diminue le succès et la portée géographique de ce processus, au travers de mécanismes évolutifs. De plus, les coûts de la dispersion devraient varier avec le type de déplacement effectué par l'individu disperseur, et par conséquent, on peut se demander (3) quelles tactiques alternatives de dispersion un individu pourrait adopter dans un environnement contrasté. Au cours de ce doctorat, mon objectif était de travailler sur ces trois hypothèses en utilisant deux jeux de données portant sur deux populations de chevreuils distinctes (données GPS en Haute-Garonne et données de Capture-Marquage-Recapture dans les Deux-Sèvres, France), ainsi qu'une approche par modélisation. Tout d'abord, j'ai montré que, malgré leur bonne condition physique, les disperseurs subissent des coûts de mortalité, reproduction et croissance. J'ai également montré que le changement climatique pourrait augmenter les coûts de mortalité chez ces individus. Parallèlement à ces variations de coûts, j'ai aussi mis en évidence que la dispersion avait diminué au cours des 30 dernières années de plus de 30% chez les deux sexes. Ensuite, j'ai identifié l'existence d'au moins six tactiques alternatives de dispersion chez le chevreuil, caractérisées par des phénologies, durées et amplitudes différentes, ce qui pourrait induire différentes répercussions en termes de coûts et de dynamique de population. Enfin, mes analyses de modélisation suggèrent que la dispersion pourrait évoluer de sorte à observer davantage de mouvements tortueux ou de courte distance quand les coûts de mortalité augmentent, ce qui limiterait la portée géographique de la dispersion. De façon générale, ces résultats soulignent les effets préoccupants que les changements globaux pourraient avoir sur les coûts et sur l'évolution de la dispersion. Ce processus étant à la fois espèce et condition dépendant, davantage d'études portant sur les impacts des changements globaux sur les coûts de la dispersion, idéalement prenant en considération les tactiques alternatives de dispersion, nous permettront de mieux prédire comment les espèces pourraient faire face aux changements globaux.

Abstract:

Natal dispersal is a process by which individuals move from their natal to reproductive ranges which is fundamental for population dynamics and persistence. Through for example the limitation of inbreeding or the capacity it provides to reach and colonize new habitats containing resources or mates, it can be highly beneficial to dispersing individuals. However, dispersal can also be costly for the individuals, through increased mortality or attrition, energy expenditure, or lost habitat opportunities and time. Its expression at the population level thus depends on the balance between costs and benefits, and theory states that dispersal may become counter-selected if costs outweigh benefits. In the current context of global change, we may expect (1) dispersal costs to increase with the degradation of environments and (2) increased dispersal costs to decrease dispersal success and geographical reach through evolutionary mechanisms. Moreover, because dispersal costs may vary with actual dispersal movement, we may wonder what are the discrete alternative tactics roe deer may use in contrasting environments (3). In this PhD, I aimed to address these three perspectives using two roe deer datasets from two geographically distinct populations (GPS data in Haute-Garonne and Capture-Mark-Recapture data in Deux-Sèvres, France), as well as a modelling approach. First, I show that, despite having a good body condition, dispersers incur costs in terms of mortality, reproduction and growth, and that climate change may increase mortality costs. Concomitant to these variations in costs, I also found that realised dispersal has diminished over the past 30 years by more than 30% in both sexes. Second, I identified at least six alternative dispersal tactics in roe deer, characterised by different movement timing, amplitude and duration, which may imply different outcomes in terms of costs and population dynamics. Lastly, my analyses suggest that dispersal might evolve towards tortuous and short distance movements when mortality costs increase, limiting the geographical reach of dispersal. Overall, these results highlight the concerning effects global changes may have on dispersal costs and dispersal evolution. Because dispersal is a species and context dependent process, more studies addressing the impacts of global changes on dispersal costs, ideally incorporating alternative dispersal tactics, will provide valuable information to better predict how species may cope with environmental changes.